Sex, Cooperation, and Deception: Anti-Predatory Behavior Beyond Avoiding Death

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CONTENTS

SUMMARY

Anti-predatory behaviors primarily serve to avoid death, but they can also serve secondary functions, such as parental care, cultural transmission, and/or advertising phenotypic quality. The understanding of how animals use their anti-predatory strategies beyond their own survival has been an overlooked aspect of widespread adaptations that may also influence the social relationships between individuals. The selective processes through which secondary functions of anti-predatory behaviors have arisen remain unresolved. This thesis explores the realm of anti-predatory behaviors in a variety of contexts. I investigate species-specific constraints of mobbing predators, the use of anti-predatory behaviors as signals of phenotypic quality in birds and primates, and how a social bird species avoids being deceived by false alarm calls. In **Chapter One** I present a general introduction of this work, with an overview of the function of anti-predatory behaviors beyond avoiding predation.

Mobbing is one of the most curious anti-predatory behaviors, where potential prey approach and harass a non-hunting predator. Although this behavior can be effective to reduce the short- and long-term predation risk, not every species engages in mobbing. In **Chapter Two** I use a field experiment in birds to explore the factors that are associated with engaging in mobbing. The results of this experiment show that species that mob have smaller body mass than non-mobbers, and also forage in safer niches (understory and canopy), and form groups, while non-mobbers are usually ground-dwellings and less likely to form flocks. Moreover, species that can afford to mob predators adjust their mobbing behavior according to the predator type by forming larger mobbing assemblages when facing a high-risk predator, or mobbing more intensely when facing a low-risk predator.

Clearly, mobbing can serve secondary functions beyond moving a predator away. Given that this behavior is risky, it has been suggested that it could also serve as an opportunity for individuals to advertise their phenotypic quality to conspecifics. In **Chapter Three** I test this idea with a field experiment in a bird community, aimed at understanding

the influence of sex-specific audience effects on mobbing behavior. The results of this experiment indicate that males mob more intensely when more conspecific females are present in the mobbing assemblage, while the audience did not influence the mobbing behavior of females. This finding provides the first empirical evidence for the hypothesis that mobbing can be used as an opportunity to signal phenotypic quality to potential mates.

In gregarious animals, anti-predatory behaviors, such as vigilance, mobbing, and counter-attacks, are beneficial for the whole group. Therefore, those behaviors could be seen as a cooperative public service. In **Chapter Four**, I test the prediction that anti-predatory services are sexually selected in primates. The results show a persistent male bias in vigilance, mobbing, and counter-attacks, suggesting that this kind of service is indeed sexually selected. The mechanisms through which sexual selection operate remain unclear. Nevertheless, this novel finding suggests that some cooperative acts, such as anti-predatory behaviors, are influenced by sexual selection, and are likely to affect mate choice and reproductive fitness.

Even though anti-predatory behaviors can be beneficial to other group members, they can also provide an opportunity to deceive others. For example, in some species, individuals may give alarm calls in the absence of a predator to gain access to food. While previous research has focused on the deceptive use of alarm calls and their benefits for the caller, it remains unclear whether call recipients have evolved counter-adaptations to overcome deception. In Siberian jays *Perisoreus infaustus*, a family-living bird species, mainly neighbor individuals give alarm calls in the absence of predators to gain access to food. In **Chapter Five** I experimentally demonstrate that jays consider signaler reliability to overcome deception. Jays immediately flee and take longer to return after being exposed to warning calls of former group members, compared to warning calls from neighbors or unknown individuals. These results suggest that Siberian jays assess reliability based on individual identity and previous relationships. This finding is the first evidence of long-term memory associated with a strategy to overcome deception in animals. Generally, this rule

may facilitate the evolution of complex communication systems, where signals provide transmutable information, such as language.

Anti-predatory strategies may not only be related to survival *per se*, but also to direct and/or indirect fitness benefits. The results presented in this thesis reveal that secondary functions of anti-predatory behaviors in birds and primates may have been sexually selected, providing novel insights into costly signaling theory and the evolution of cooperation. Moreover, the evidence that birds may use reputation and reliability to deceive and avoid deception suggests novel paradigms for the understanding of the evolution of complex communication systems such as human language.

ZUSAMMENFASSUNG

Die primäre Funktion von Antiprädationsverhalten ist es, den Tod zu vermeiden; jedoch kann es auch sekundäre Funktionen erfüllen, z.B. elterliche Fürsorge, kulturelle Transmission und das Anzeigen phänotypischer Qualität. Diese Dissertation erforscht die Ausprägung von Antiprädationsverhalten in verschiedenen Kontexten. Ich untersuche hier artspezifische Einschränkungen von Raubtiermobbing, den Gebrauch von Antiprädationsverhalten als Signal phänotypischer Qualität in Vögeln und Primaten, sowie das Vermeiden von Täuschungen durch falsche Alarmrufe in einer sozialen Vogelart. **Kapitel Eins** bietet eine Übersicht über Antiprädationsverhalten jenseits der direkten Vermeidung von Fressfeinden.

Mobbing ist eines der interessantesten Antiprädationsverhalten, bei dem potentielle Beutetiere sich einem nichtjagenden Fressfeind annähern und diesen bedrängen. Obwohl dieses Verhalten effektiv sein kann, kommt es nur in wenigen Arten vor. In **Kapitel Zwei** ergründe ich die limitierenden Faktoren der Teilnahme an Mobbing anhand eines Feldexperiments bei Vögeln. Die Resultate dieses Experiments zeigen, dass Arten welche mobben von ihrer Körpermasse eine potentielle Beute sind, in sichereren Mikrohabitat nach Futter suchen und in Gruppen leben. Arten passen ihr Verhalten dem Risiko an welches vom Prädator ausgeht und mobben einen weniger gefährlichen Prädator intensiver als einen gefährlicheren Prädator.

Mobbing kann sekundäre Funktionen annehmen. Zum Beispiel kann dieses Verhalten als. Gelegenheit für Individuen dienen könnte, Artgenossen ihre phänotypische Qualität anzuzeigen. In **Kapitel Drei** teste ich diese Idee mit Hilfe eines Feldexperiments. Die Resultate dieses Experimentes zeigen, dass Männchen intensiver mobben je mehr weibliche Artgenossen anwesend sind. Dieses Ergebnis ist die erste empirische Evidenz dafür dar, dass Antiprädationsverhalten als Gelegenheit genutzt wird, potentiellen Paarungspartnern phänotypische Qualität anzuzeigen.

In sozialen Tieren haben Antiprädationsverhalten wie Wachsamkeit, Mobbing und Gegenangriffe einen Nutzen für die gesamte Gruppe. Entsprechend könnten diese Verhalten als kooperative gemeinnützige Dienste angesehen werden. In **Kapitel Vier** teste ich die Hypothese, dass solche Verhaltensweisen bei Primaten das Resultat sexueller Selektion sind. Die Ergebnisse zeigen, dass Wachsamkeit, Mobbing und Gegenattacken in Männchen durch sexuelle Selektion beeinflusst wird. Dieser Befund zeigt, dass einige kooperative Handlungen wie Antiprädationsverhalten von sexueller Selektion beeinflusst sind und somit Partnerwahl und Fitness beeinflussen.

Obwohl Antiprädationsverhalten in sozialen Arten üblicherweise allen Gruppenmitgliedern nutzt, könnten diese Verhalten benutzt werden um andere zu täuschen. In vielen Arten machen Individuen Alarmrufe in Abwesenheit eines Räubers, um Zugang zu Nahrung zu erhalten. Während sich die bisherige Forschung auf den irreführenden Gebrauch von Alarmrufen und deren Nutzen für den Rufer fokussiert hat, bleibt unklar ob Rufempfänger Gegenstrategien entwickelt haben, um diese Täuschung zu überwinden. In **Kapitel Fünf** untersuche ich anhand eines Feldexperiments einen Mechanismus zur Täuschungsvermeidung in einer sozialen Vogelart, dem Unglückshäher. Individuen reagierten sofort auf Alarmrufe ehemaliger Gruppenmitglieder, nicht aber auf Nachbarn oder unbekannte Individuen, welche häufig falsche Alarmrufe abgeben, um Zugang zu Nahrung zu erhalten. Die Resultate zeigen, dass die Beziehungen entscheidend ist, um die Zuverlässigkeit eines Signals zu beurteilen.

Die Resultate dieser Dissertation zeigen, dass Antiprädationsverhalten auch sekundäre Funktionen einnehmen können und der Partnerwahl dienen können. Zudem benutzen Vögel eine einfache Regel um den Missbrauch von Alarmrufen zu verhindern, indem sie nur Rufen von bekannten Individuen vertrauen. Diese einfache Regel ermöglicht der Evolution komplexer Kommunikationssysteme, einschliesslich Sprachen.

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During this thesis, much work in the field was done, some you may read here, some you may read somewhere in the near future. During the fieldwork I had the support of lots of people to whom I am deeply grateful for it: Julian Klein, Charlotte Wroblewski, Maravillas Miñano, Anne Ausems, Sonja Falkner, Jessica Winter, Christian Kaula, João Biagini, Rafael Lara, Encarni, “Manolo”, Manolo, Inês García, Rafa, and “Pepe”.

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It was fun.

CHAPTER ONE

Thesis Overview

Filipe C. R. Cunha

General Introduction

The battle for staying alive is ubiquitous in the animal kingdom. Most animals are preyed upon by others and therefore predation avoidance pervades evolution. The evolutionary processes between predator and prey are analogous to an arms race (Dawkins and Krebs 1979), where the prey's adaptations to avoid death coevolve with predators' traits (i.e., hunting tactics). This evolutionary arms race results in distinct outcomes for both sides. On an ecological time scale, predators that lose the race lose a meal, while prey that lose the race lose their life. Therefore, predators impose an important selective pressure on prey, which, in turn, evolve diverse strategies to survive.

A hunting predator must locate a prey before capturing it, thus avoiding detection is the first line of defense against predators. Many animals evolved coloration that match the color of the environment (i.e., camouflage), reducing the risk of being detected by predators (Steward 1977; Stevens and Merilaita 2011) (Figure 1.1a). Although camouflage is efficient to avoid detection (Pietrewicz and Kamil 1977; Stuart-Fox et al. 2006), it is costly (Rodgers et al. 2013), and often imposes limitations on movement (Cott 1940; Huffard 2006). Alternatively, prey may look inedible, by having a color pattern that conveys such information (i.e. aposematism (Figure 1.1b)), (Poulton 1890), or by mimicking unpalatable species (Bates 1862).

Another tactic to avoid detection is vigilance, where prey actively scan their surroundings for predators (Figure 1.1c) (Fitzgibbon 1990). The effectiveness of vigilance

depends on detecting a predator before being detected or surprised by one. While scanning its surroundings, an individual cannot engage in other activities, such as foraging, moving, or social interactions (Coolen and Giraldeau 2003), and therefore there is an inherent cost to being vigilant (Illius and Fitzgibbon 1994; Cowlishaw et al. 2004).

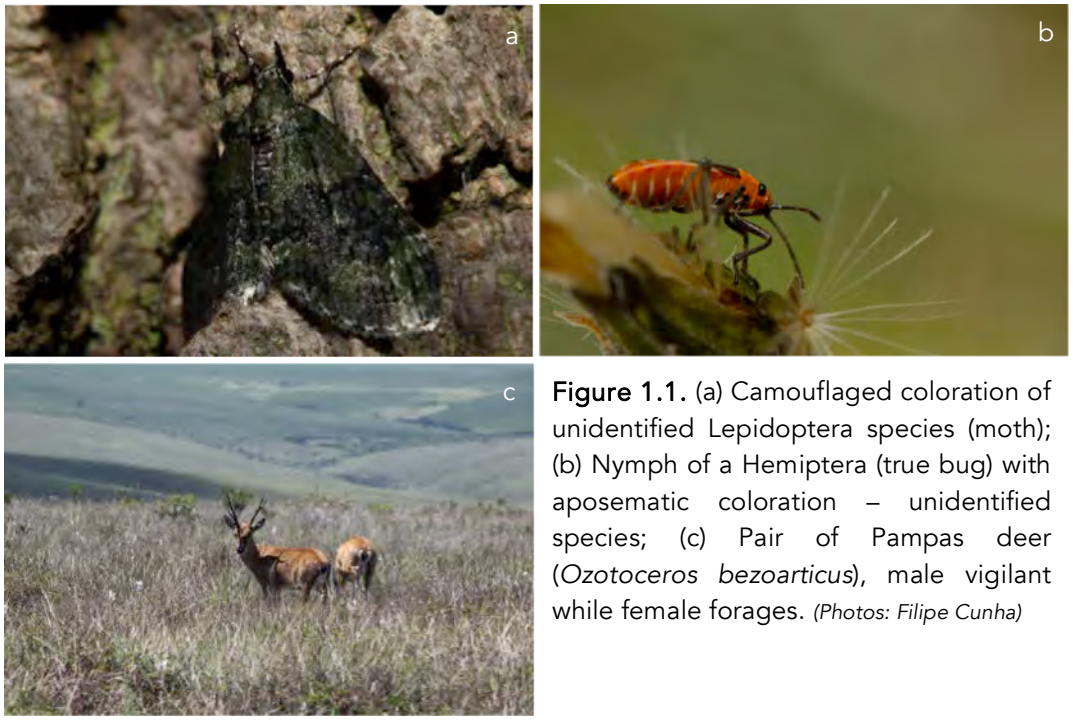

Figure 1.1. (a) Camouflaged coloration of unidentified Lepidoptera species (moth); (b) Nymph of a Hemiptera (true bug) with aposematic coloration – unidentified species; (c) Pair of Pampas deer (*Ozotoceros bezoarticus*), male vigilant while female forages. *(Photos: Filipe Cunha)*

Predators can overcome their prey's adaptations to avoid detection and make an individual its target. Accordingly, prey have evolved strategies to avoid capture. Escape is a conspicuous form of avoiding capture, requiring adaptations that allow a fast reaction and rapid getaway (Domenici 2001; Husak 2006). Prey have to overcome the predator in pursuit by being faster (Husak 2006; Elliott et al. 2011), having more endurance (Vanhooydonck et al. 2009; Elliott et al. 2011), and/or making unexpected moves (Howland 1974; Domenici et al. 2011) until finding refuge or outrunning the predator. Some species have evolved weaponry to avoid being captured (Caro 2005; Stankowich and Campbell 2016). The crested porcupine (*Hystrix cristata*), for example, will present their spiny coat to a predator, while bombardier beetles (*Brachinus* sp.) will spray predators with a high-temperature toxic substance.

Given that anti-predatory behaviors aim at avoiding injury and death, deliberately approaching a predator is an unexpected behavior for a prey. However, in one peculiar anti-predatory behavior, potential prey approach a predator to harass and attack it (Hartley 1950; Shields 1984). This puzzling behavior, known as mobbing (Figure 1.2), is a widespread strategy (Altmann 1956; Caro 2005). Although mobbing is adaptive (Curio et al. 1978a), because it is used to move the predator away (Flasskamp 1994), reducing the immediate predation risk (Pavey and Smyth 1998), it can also be deadly (Motta-Junior 2007). Species' ecological traits may impose constraints on the expression of mobbing since the costs and benefits may differ among taxa. Thus, it is expected that not every species can afford to expose itself to such a risky situation with a predator (*see* **chapter two**). Moreover, for those species that do mob, ecological constraints and different risks posed by distinct predators, influence potential prey to adjust their mobbing strategy according to the situation (*see* **chapter two**).

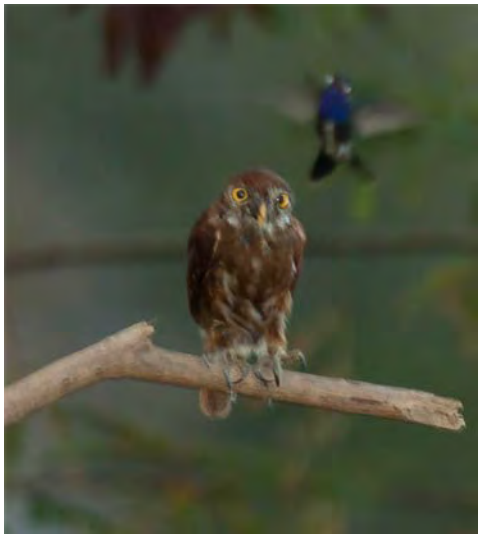

Figure 1.2. A Sapphire-spangled emerald (*Amazilia lactea*) mobbing a taxidermized model of a Ferruginous Pygmy-owl model (*Glaucidium brasilianum). (Photo: Filipe Cunha)*

After a predator strikes, prey can counter-attack instead of escaping (Tello et al. 2002; Gardner et al. 2015). Counter-attacking is not only energetically costly, but is quite risky because in these situations the predator is hunting, and is likely to take additional victims to protect its prey. However, in such events, prey may not only persuade a predator, but can also kill it (Boinski, 1988). When a counter-attack is executed by an individual other than the one initially attacked, it is essentially a cooperative behavior aimed at rescue. In primates, for example, mothers can rescue their offspring after they have been attacked by snakes (Corrêa and Coutinho 1997, Quintino and Bicca-Marques 2013). Ecological factors may play a role in the expression of this behavior, given that not every prey can afford to face a more powerful predator. While it is possible to observe

Cape buffalo (*Syncerus caffer*) facing lions (*Panthera leo*), an arctic hare (*Lepus arcticus*) will never counter-attack a pack of arctic wolves (*Canis lupus arctos*).

A last line of defense is to avoid consumption. For that, prey can feign death, a behavior known as thanatosis (Gilman et al. 1950). Many predators will not consume prey that they have not killed. Thanatosis is a widespread behavior used as a last resort to avoid death (Caro 2005). The Virginia opossum (*Didelphis virginiana*), for example, will feign its' own death if threatened by a predator. As soon as the predator loses interest, the opossum will seek a safe refuge. Although considered adaptive (Thompson et al. 1981), little is known about the general effectiveness of this behavior. Animals have also evolved structures that can prevent their consumption, such as armor, shells, or spikes. For instance, a Pangolin's (*Manis* sp.) scales can protect it from lions even after being captured.

Clearly, the primary function of anti-predatory behaviors is to prevent oneself or one's offspring from getting killed. However, these behaviors can assume secondary functions like cultural transmission of predator recognition (Vieth et al. 1980), social monitoring of potential competitors for mates (Baldellou and Peter Henzi 1992), and as costly signaling (Zahavi 1995) for potential partners in dispersal coalitions (Maklakov 2002) (Table 1.1). The latter is enhanced in social species, in which anti-predatory behaviors can be seen as a public good and an opportunity for social interactions (Gintis et al. 2001; Maklakov 2002). Moreover, given that anti-predatory behaviors are costly, it has been suggested that they could be used to convey honest signals of phenotypic quality (Zahavi 1995) (see **chapter three**). Costly signaling is commonly associated with extravagant ornaments used by males to advertise their quality to choosy females. However, costly signals of phenotypic quality could also be expressed through anti-predatory behaviors, during which an individual could advertise its ability to detect and/or face predators, providing an important safety service (see **chapter four**)

Table 1.1. Active anti-predatory behaviors: primary and secondary functions.

anti-predatory behavior	primary function	secondary function
escaping	seek refuge, signal strenght[1]	-
vigilance	detect predator[2], warn others*[3]	social monitoring[7], advertise phenotypic quality[8]
mobbing	move the predator away[4]	cultural transmission[9], enhance social bonds[10], advertise phenotypic quality[8]
counter-attacking	self-defense, rescue of others[5]	advertise phenotypic quality[8]
thanatosis	avoid consumption[6]	-

[1] (Smythe 1970; FitzGibbon and Fanshawe 1988); [2] (Pulliam 1973); [3] (Klump and Shalter 1984); [4] (Curio et al. 1978b); [5] (Boinski 1988); [6] (Gilman et al. 1950); [7](Baldellou and Peter Henzi 1992); [8] **chapter three** and **four;** [9] (Curio et al. 1978a); [10] (Krams et al. 2008); * Although warning signals are prevalent in vigilance, principally in gregarious species, this adaptation can be present in all anti-predatory behaviors, except thanatosis. Here, "warning others" is added as a function only for vigilance, because it is not contingent of the other behaviors listed.

While in group-living species anti-predatory services usually produce a public good, namely safety, individuals can also use these behaviors as opportunities to deceive others. In group-living species, anti-predatory behaviors demand a communication system, which can be used to alert others of a threat, like warning calls for example (Klump and Shalter 1984). Although warning calls are mainly used to inform others about a dangerous situation (Caro 2005), they can also be used to deceive (Munn 1986; Flower 2011). Deception, which consists of falsifying a signal, thereby provoking a reaction from others, is one of the most intriguing usages of a communication system. The aftermath of this deceitfulness is contingent on the receiver's reaction, since a receiver would only pay costs if it reacts as if the signal was honest (Møller 1988). Given that receivers pay costs of deception, mechanisms to avoid deception are expected to evolve (see **chapter five**). However, little is known about false warning calls and corresponding counter-deception mechanisms. In fact, although the deceptive use of warning calls have been described for some species (Munn 1986; Møller 1988; Wheeler 2009; Flower 2011), no mechanism of counter-deception has been described.

Anti-predatory behaviors are about more than just avoiding death, and this thesis presents novel insights into their function. In this thesis, I explore the limiting factors for

species to engage in mobbing behavior, the selective processes through which anti-predatory behaviors may have evolved, and how a bird species can avoid deception.

Aims and outline of thesis

Not all birds mob

Although mobbing is commonly observed, not all species mob their predators, and the limiting factors of engaging in this behavior remain unknown. In **chapter two** I investigated the role of social and ecological traits for the expression of mobbing behavior with a field experiment in a bird community in SE Brazil (n=157 species) (Appendix 2.1). I presented models of two morphologically similar diurnal owls that pose different risks to birds: a Ferruginous Pygmy-owl model (*Glaucidium brasilianum*) which mainly eats small birds, and therefore poses a high risk (Figure 1.3a), and a Burrowing Owl model (*Athene cunicularia*) which mainly eats insects, and therefore poses a low risk (Figure 1.3b). I then assessed which species engaged in mobbing these models. Among those that mobbed, I evaluated how they adjusted their mobbing behavior to the predator type. This is the first comparative study on the expression of mobbing behavior in birds.

Figure 1.3. (a) Ferruginous Pygmy-owl (*Glaucidium brasilianum*); (b) Burrowing Owl (*Athene cunicularia*). *(Photos: Filipe Cunha)*

Specifically, I tested the hypothesis that only species that are both at risk and can afford to mob engage in this anti-predatory behavior. Using phylogenetically controlled mixed models, I tested whether a species' engagement in mobbing could be predicted by body mass, foraging strata, flocking habits, or social system. The results indicate that species that engaged in mobbing have smaller body mass than non-mobbers (Figure 2.1a). In addition, mobbers forage in the understory or in the canopy (Figure 2.1b), and form flocks (Figure 2.1c), while non-mobbers are ground-dwelling and are less likely to form flocks. However, a species' social system did not predict engagement in mobbing behavior. Furthermore, species adjusted their mobbing behavior in accordance to the risk posed by each predator. Birds formed larger mobbing assemblages when facing a high-risk predator (Figure 2.2), while they mobbed more intensely when facing a low-risk predator (Figure 2.3). The findings presented in **chapter two** provide novel insights into the factors that facilitate the evolution of mobbing behavior, showing that only species that are potential prey but can afford to mob express this behavior.

Risky behaviors as costly signals

Animals may use the expression of anti-predatory behaviors as costly signals. In **chapter three**, I test the idea that male birds may use mobbing as an opportunity to advertise their phenotypic quality. To this end, I carried out a field experiment in SE Brazil and assessed the response of 19 sexually dimorphic bird species to models of two diurnal owls that pose different risks to birds: a Ferruginous Pygmy-owl (high-risk), (Figure 1.3a), and a Burrowing Owl (low-risk) (Figure 1.3b). Overall, individuals mobbed the low-risk predator more intensely than the high-risk one (Figure 3.1). Moreover, across the 19 species, more males (n=108) engaged in mobbing than females (n=57). Interestingly, the mobbing intensity of males was higher when a larger number of conspecific females were present in the mobbing assemblage (Figure 3.2). This novel finding suggests that sex-specific asymmetry in mobbing behavior may be due to males using mobbing as an opportunity to advertise their phenotypic qualities to females.

In group-living species anti-predatory behaviors often provide benefits to the whole group. These cooperative acts regarding safety have been hypothesized as an opportunity to advertise one's quality as a cooperative partner (Gintis et al. 2001; Maklakov 2002). In **chapter four** I investigated if acts of assistance towards unrelated individuals without evidence of reciprocation in kind (services) are sexually selected in primates. A male bias in anti-predatory behaviors has been reported in some species, but there has been no systematic analysis to examine whether this bias is a broad trend among primates or how its strength relates to mating systems. In this study I investigated if there is sex-specific asymmetry in anti-predatory services in primates. I compiled published data on vigilance, mobbing, and counter-attacks and assessed if there is a predominant sex bias in these behaviors. I calculated a measurement of the participation of adult males and females in each behavior by using an index reflecting the sexual bias in participation (see **chapter four**).

Overall, I assembled data from 39 primate species. The results demonstrate a highly prevalent male bias in all anti-predatory behaviors tested (Figure 4.1a-c), indicating that such services are not reciprocated in kind, but should bestow other benefits to males, like mating access. Although parental care may play a role on the pervasiveness of this male bias, it is unlikely to be the explanation for this pattern, since females, which have more certainty of parenthood, are not more active in offspring defense than males. Paternal care does not provide an explanation for multi-male counter-attacks in which different males participate with similar contributions (e.g., Boesch 1991, Cowlishaw 1995). Furthermore, I examined whether the observed patterns could be explained by the species' mating system, while controlling for phylogeny, sexual size dimorphism, predator type, and niche substrate. Surprisingly, the mating system did not explain the strength of male bias in any of the behaviors tested and the covariates did not present a significant relationship with the male bias in vigilance or mobbing. Yet, for counter-attacks, only predator type (Figure 4.2a) and sexual size dimorphism (Figure 4.2b) presented a significant relationship with the strength of the male bias. The male bias was stronger for counter-attacks against

Figure 1.4. (a) Siberian jay (*Perisoreus infaustus*) on the feeder during experiments; (b) Siberian jay (*Perisoreus infaustus*). *(Photos: Filipe Cunha)*

mammalian and avian predators, compared to snakes. This may be because counter-attacks against snakes are less risky, and presumable mothers attempt to rescue their offspring. When males are bigger than females (greater sexual size dimorphism) they are also better equipped to deal with predators, which may be most relevant for engangement in counter-attacks, the riskiest behavior of the three tested.

Taken together, the findings of **chapters three** and **four** suggest that anti-predatory behaviors may have been sexually selected, given that there is a sex-specific asymmetry in the expression of it. Males may particularly use these anti-predatory behaviors as opportunities to advertise their quality as a mate and/or as a cooperative partner.

The birds that "cry-wolf"

Anti-predatory signals, like warning calls, are not always honest. In C**hapter five** I present the findings from a field experiment on how a bird species, the Siberian jay (*Perisoreus infaustus*) (Figure 1.4a and 1.4b), deals with deception. This species lives in family groups on joint territories and relies on group members for their safety and to defend their resources from intruding neighbors. In Siberian jays, individuals from neighboring groups

sometimes give warning calls in the absence of predators to gain access to food (Appendix 5.1).

I conducted a series of playback experiments broadcasting warning calls from former group members, neighbors, and unknown individuals to adult Siberian jays. Siberian jays responded immediately to playbacks of warning calls of former group members but not to warning calls of neighbors or unknown individuals. These findings suggest that individuals trust the warning calls of relatives and familiar individuals with whom they share or have shared common interests. Neighbors are those that most often use warning calls in a deceptive manner and accordingly, breeders do not react immediately to their warnings. The findings from **chapter five** indicate that Siberian jays have a long-term memory of past social relationships, allowing them to discriminate between reliable and unreliable callers. This simple rule helps individuals to overcome communicative deception.

Final Remarks and Prospectus

Organisms must carefully weigh the costs and benefits of engaging in anti-predatory behaviors (**chapter two**), influencing their evolution. Moreover, the secondary functions of these behaviors are often overlooked. In this thesis I present novel findings that suggest that anti-predatory behaviors can be used as costly signals of phenotypic quality. In birds, males use mobbing behavior as an opportunity to advertise their phenotypic quality (**chapter three**), and in primates, males seem to use anti-predatory behaviors to advertise their quality as cooperative partners (**chapter four**). These findings suggest that cooperative anti-predatory behaviors are sexually selected, which calls for a rethinking of the evolution of cooperative behaviors. However, anti-predatory behaviors are not always cooperative, and some social species may use warning signals to deceive others. The evidence that birds can determine caller reliability as a strategy to avoid deception (**chapter five**) suggests novel paradigms for the understanding of the evolution of complex communication systems such as human language. Overall, these new avenues for the

study of the evolution of anti-predatory behaviors reveal that the social implications of avoiding predation deserve more attention.

Clearly, additional empirical tests are needed to better understand the mechanisms through which sexual selection influences the evolution of anti-predatory behaviors. Although mobbing is only beneficial for potential prey (see **Chapter Two**), the secondary functions of this behavior could impose variation on its expression. The results presented in this thesis suggest that males use anti-predatory behaviors as an opportunity to advertise their quality to potential mates, supporting a previous theoretical proposal (Dugatkin and Godin 1992). However, it is still unclear if males that engage most in these behaviors are indeed the stronger ones (as honest signals of phenotypic quality (Zahavi 1975)), or if weaker males assume these risks to compensate for undesirable phenotypic traits (as an alternative mating tactic (Taborsky et al. 2008)). Either way, variation in the expression of anti-predatory behaviors among individuals is expected (Shedd 1983; Regelmann and Curio 1986; Francis et al. 1989; Maklakov 2002; Griesser and Ekman 2005), but the approach of the studies in this thesis did not allow further exploration of this hypothesis. In **chapter three** I have shown a sex-specific audience effect in mobbing, yet it remains unknown if females choose their mate based upon this show of bravado. Moreover, empirical investigation into the fitness consequences of engaging in risky behaviors is needed.

In **chapter four** we present novel evidence that a form of cooperative behavior is sexually selected. The evolution of cooperation remains one of the most challenging questions in biology. Although sexual asymmetry in cooperative behaviors has been observed (Rose and Fedigan 1995; Eckardt and Zuberbühler 2004; Ouattara et al. 2009), sexual selection has been largely ignored as an explanation for the evolution of these behaviors in non-human animals. Anti-predatory behaviors in social animals provide a unique opportunity to study the evolution of cooperative acts, since defecting in this scenario can be deadly for the defector, its relatives and/or its potential mates.

Even though our results show that mating systems do not influence male participation in anti-predatory behaviors in primates, it may play a role in individual motivation to take higher risks (Dugatkin and Godin 1992). Female choice may influence the expression of anti-predatory behaviors (**chapter three** and **four**). Males advertising their vigor to potential mates may be more prevalent in species with greater female choice (e.g., multi-male groups). Thus, in species with the highest paternity assurance (e.g., monogamous pairs) the expression of anti-predatory behavior may be driven by paternal care, but equally, by males avoiding divorce. Empirical validation of the hypothesized link between male engagement in anti-predatory behaviors and fitness are needed for better understanding of the evolutionary mechanisms involved.

Finally, this dissertation provides a unique glimpse into a communication system tinged with chicanery, in a field experiment with a wild population of Siberian jays. In **chapter five** we explore how a bird species avoids being deceived using an intricate rule of reliability based on shared survival stakes. We suggest that this mechanism requires the cognitive ability to evaluate the meaning of a signal (Griesser 2008) against the caller's reputation (Wascher et al. 2015). We observed that individuals from neighboring territories emit warning calls in the absence of predators more frequently than others, but the conditions in which deception takes place deserve further investigation. Siberian jays live in year-round territorial family groups, and non-related immigrants integrate into the familiar groups either as juveniles in dispersal, or as vagrant adults. Juveniles are unfamiliar with predators (Griesser and Suzuki 2016) and do not know the appropriate meaning of warning calls, and are therefore unlikely to attempt to deceive others. Vagrant adults, however, are more experienced, and could use warning calls in a deceptive manner.

Further field experiments are needed to understand how birds perceive the opportunities to deceive. New adult immigrants are initially not familiar, and as our results suggest, these birds should be ignored if they try to deceive others. However, after a certain time these adult immigrants start to share survival stakes with others and to become part of the group. They can assume distinct positions in the group from being

tolerated by the dominant breeding pair to a marginal position. The social ranking of an individual may influence its motivations to deceive, given that marginal immigrants have fewer opportunities on food sources. Moreover, the results revealed a higher variance on the response to warning calls of neighbors than of unknown individuals. This suggests that the individual relationships amongst neighbors influence how reliability is judged. Further field observations and experiments can elucidate the intents and motivations to deceive, and reveal new understanding of the causes and consequences of deception in social groups.

Taken together, the findings presented in this thesis provide insights for future studies on anti-predatory behaviors, sexual selection, cooperation, and communication. The results of this thesis suggest that anti-predatory behaviors are a sexually selected, in primates as a form of cooperation, and in birds as an opportunity by male birds to advertise their phenotypic quality. Moreover, birds determine an individual's reliability to avoid being deceived by false alarm calls. Further empirical and theoretical studies are needed to answer the questions that arose from this work.

CHAPTER TWO

Predation risk drives the expression of mobbing across bird species

Filipe C.R. Cunha[1,2], Julio C.R. Fontenelle[3] and Michael Griesser[1,4]

Many species approach predators to harass and drive them away, even though mobbing a predator can be deadly. However, not all species display this behavior, and those that do can exhibit different behaviors while mobbing different predators. Here we experimentally assessed the role of social and ecological traits on the expression of mobbing behavior in a bird community in SE Brazil (n=157 species). We exposed birds to models of two morphologically similar diurnal owls that pose different risks, and assessed which species engaged in mobbing. Among those that mobbed, we evaluated how they adjusted their mobbing behavior depending on the predator type. We tested the hypothesis that only species that are at risk and can afford to mob engage in this anti-predator behavior. We found that species that engaged in mobbing are in the body mass range of potential prey, forage in the understory or in the canopy, and form flocks. A species' social system did not influence its mobbing behavior. Furthermore, species that engaged in mobbing formed larger mobbing assemblages when facing a high-risk predator, but mobbed more intensely when facing a low-risk predator. Our findings support our predictions, namely that the expression of mobbing is limited by its costs.

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Introduction

Predation is an important selective force, facilitating the evolution of anti-predatory adaptations, such as mobbing behavior. During mobbing, potential prey approach a potential predator to harass and sometimes even attack it, with the primary function of driving the predator away (Curio et al. 1978a; Caro 2005). Thus, mobbing is likely to be adaptive (Curio et al. 1978a; Vieth et al. 1980), reducing the immediate risk for the mobber (Pavey and Smyth 1998). Moreover, moving-on a predator may limit the future risk of attacks (Flasskamp 1994). However, mobbing can be costly since predators may kill prey during mobbing (Sordahl 1990; Motta-Junior 2007).

A large number of field studies investigated the costs and benefits of mobbing in single species, showing that this behavior can increase the chances of survival for the mobber, their offspring, and their relatives (Shields 1984; Pavey and Smyth 1998; Griesser and Suzuki 2017). Also, mobbing can serve as an opportunity to recruit partners for future mobbing events (Krams et al. 2008). Generally, it is expected that the costs and benefits of mobbing vary across species, influencing its expression (Dugatkin and Godin 1992; Pavey and Smyth 1998; Krama and Krams 2005). However, we lack comparative studies that investigate the influence of ecological and social traits on the expression of mobbing across species, and how these factors influence this behavior depending on the risk posed by a predator. Accordingly, it remains unclear why only some species but not others engage in mobbing when encountering certain predators.

Here we take a comparative, phylogenetically-controlled approach to assess correlates of mobbing behavior in birds. We exposed a bird community in SE Brazil to models of two diurnal perch-hunting owls that differ in their risk. We examined which social and ecological traits are associated with engagement in mobbing, testing four non-exclusive hypotheses:

i) Size matters hypothesis: We predicted that only species that are potential prey should engage in mobbing. Predators can only kill prey of a given body size

(Valcu et al. 2014), and thus only species that fall within the size range of potential prey should engage in mobbing.

ii) Safe niche hypothesis: We predicted that ground-dwelling species should be less likely to mob perch-hunting owls than species that forage in the understory or canopy. Ground-dwelling species are more vulnerable to perch-hunting predators with a top-down hunting strategy (Ekman 1986; Suhonen 1993), as they are more easily killed by these predators and have less possibilities to escape in case of an attack.

iii) Safety in numbers hypothesis: We predicted that being in a group minimizes the per capita risk of being killed (Hamilton 1971, Hogan et al. 2017). Thus, solitary species are less likely to mob than group-living and flocking species due to the higher risk during mobbing.

iv) Social facilitation hypothesis: We predicted that mobbing may provide a social learning opportunity to recognize predators (Curio et al. 1978b) for family members (Griesser and Suzuki 2016, Griesser and Suzuki 2017). Thus, family living species (including cooperative breeders; Griesser et al. 2017) are predicted to mob more than non-family living species.

Furthermore, among the species that do engage in mobbing, we tested the 'mobbing plasticity hypothesis', which predicts that birds can recognize the risk posed by predators (Caro 2005) and adjust their mobbing behavior accordingly. Thus, species that engage in mobbing are predicted to mob a more dangerous predator more intensely and in larger mobbing assemblages. Moreover, since mobbing can be used as nest defense (Arnold 2000) we predicted that birds would mob more intensely during the breeding season than during the non-breeding season (Shedd 1982; Shedd 1983).

Methods

This study was carried out on Cauaia Ranch, Minas Gerais State, SE Brazil (19°28`S 44°01`W) between February 2011 and February 2012. The study site is part of the

Environmental Protection Area Carste Lagoa Santa, where semi-deciduous forests and Brazilian savannah patches dominate the landscape, forming a mosaic of pastures, marshes, deciduous forests and temporary lagoons.

We exposed the local bird community to models of two diurnal owl species that are morphologically similar but differ in their risk to birds: a Ferruginous Pygmy-owl (*Glaucidium brasilianum*) that represents a high risk predator, i.e., 43% of its diet consists of birds (Carrera et al. 2008), and a Burrowing Owl (*Athene cunicularia*) that represents a low-risk predator, i.e., 95% of its diet consists of arthropods (Zilio 2006), but occasionally eats birds (Motta-Junior 2006). Both owls have a preference for small-sized prey: Ferruginous Pygmy-owls hunt prey weighing on average 43.7 g (min-max: 12.5-225.0 g) (Carrera et al. 2008), and Burrowing Owls hunt prey weighing on average 39.2 g (min-max: 0.07-210 g, with 60% of their diet composed of prey weighting 0.07 to 20 g) (Nabte et al. 2008).

We chose 18 experimental locations that were at least 250 m apart to reduce the risk of resampling the same individuals on the same day (Bibby et al. 2012). In each location, we performed 5-6 experiments per model following a Latin square design, resulting in 96 experiments per model. For each experiment, we selected a different location in a relatively open area on the forest edge. We placed the predator model on a 1.5 m high pole, 2 m away from an approximately 3 m high tree. We attached marks at 2, 5, 10 and 15 m in all four cardinal directions from the model, facilitating the assessment of the distance between mobbers and the model. Experimental locations were selected to allow the observer good visibility of at least 20 m in all directions around the model.

We placed a speaker on the ground below the model to playback vocalizations of the model species (30 sec calls, 15 sec silence, during 10 min) to simulate the presence of a live predator. During the experiment, an observer was positioned 10-15 m away from the model wearing camouflage clothing. We recorded the behaviors and distance to the predator model of all present individuals. All trials were conducted between 06h00 and

12h00 local time, corresponding to the time of the day with the highest activity of birds. No trials were conducted on rainy days.

We recorded all species observed in the experimental locations three minutes before each experiment (576 minutes of observation) to assess the bird species present in the study site. We also included all species that mobbed the models during the trials (1920 minutes of observation).

We obtained data on the body mass, diet, foraging strata, flocking behavior and social system of the species from handbooks (del Hoyo et al. 2015). Species were categorized according to their foraging strata: ground, understory or canopy; their flocking habits: species that live in stable group or joins flocks, or solitary species; and to their social system: non-family living, family-living (offspring delay dispersal >50 days beyond independence (Drobniak et al. 2015)), or cooperatively breeding species (Cockburn 2006). Species whose social system is unknown were not considered for the analysis including this variable.

We assigned the mobbing status of a species based on the response in all experiments using a categorical variable with two levels: i) mobber: a species that mobbed during at least one experiment; ii) non-mobber: a species that is present at the study site but was never observed mobbing).

We assessed the mobbing intensity of all individuals that engaged in mobbing on an increasing ordinal scale from 1-7 (adapted from (Chandler and Rose 1988; Motta-Junior and Santos-Filho 2012)). Mobbing intensity was ranked based on the mobber's distance from the model (in meters), and its behavior (emitting calls or not, and/or visual displays such as flapping wings, rattling the tail feathers, ruffling the crown feathers and/or repetitive movements with wings, tail or head): 1) an individual was > 10 m away from model making visual displays and/or giving warning calls or being silent, 2) an individual was ≤ 10 m and > 5 m away making visual displays and/or giving warning calls or being silent, 3) an individual was ≤ 5 m and > 2 m away being silent, 4) an individual was ≤ 5 m and > 2 m away making visual displays and/or giving warning calls, 5) an individual was ≤ 2

m away being silent, 6) an individual was ≤ 2 m away making visual displays and/or giving warning calls but not attacking the model, and 7) an individual was physically attacking the model.

Statistical Analyses

We used the software R 3.3.2 for the statistical analyses (R Core Team 2016), using Generalized Linear Mixed Models in the package MCMCglmm (Hadfield 2010). This method allowed us to perform phylogenetic regression analyses (Ives and Garland 2014) of response variables that do not follow a Gaussian error distribution. To test our hypotheses we ran three separate models to assess the influence of independent factors on i) whether species mob or not (mobbers vs non-mobbers, categorical variable with two levels), ii) the mobbing intensity (an ordinal scale (rank scale 1-7, see above), and iii) the mobbing assemblage size (a discrete numerical variable). The 'MCMCglmm' statistical R package uses Markov chain Monte Carlo (MCMC) probabilistic sampling technique, making the analysis of complex models possible (Hadfield 2012). Furthermore, the use of 'MCMCglmm' allowed us to include random variables in the models, and to control for the influence of phylogeny (Hadfield 2012; Ives and Garland 2014).

We included a consensus tree at the species level of a recent phyla-wide avian phylogeny (Jetz et al. 2012) as a random effect to control for phylogenetic non-independence. The MCMCglmm models were run for 100,000 iterations, with a 1,000 burn-in period and samples drawn every 100 iterations. Our models resulted in comparable effective sample sizes for all factors (~1000), and visual inspection of trace plots indicated proper mixing of the models.

To test the four hypotheses regarding the influence of ecological and social traits on whether or not species engage in mobbing behavior, we included the following species-specific explanatory variables into the model: body mass (log-transformed, in grams), foraging strata, flocking habits, social system. We also included the encounter rate per minute as a covariate to control for the influence of relative species abundance. We used a

categorical mixed model using the logit link function in MCMCglmm. For this model we excluded species for which the social system is unknown. Thus, the analysis was conducted with a reduced dataset of 145 species, of which 67 species mobbed.

Within the species that mobbed, we assessed the factors that influenced mobbing assemblage size and mobbing intensity with separate models. For the former, we performed a phylogenetically-controlled Poisson-distributed generalized linear mixed model with log link, using MCMCglmm. We included the following explanatory variables in this model: predator model (high-risk, low-risk), season (breeding season (September to February), non-breeding season (March to August)), and the maximum mobbing intensity during an experiment of each individual (ordinal scale from 1 to 7). To test mobbing intensity we performed a phylogenetically-controlled ordinal generalized linear mixed model with a probit function, using MCMCglmm. We included the maximum mobbing intensity of each individual as the response variable and the following explanatory variables: predator model (high-risk, low-risk), season (breeding season (September to February), non-breeding season (March to August)), and the mobbing assemblage size. In addition to phylogeny, we included in both models the location and the date of each trial as a random effect to control for repeated sampling in the same location. For these models we included all 79 species that mobbed at least once.

We used the package 'car' (Fox and Weisberg 2011), to test for collinearity using the generalized variance inflation factor (GVIF) (Appendix 2.2), which revealed that the factors in our models have a low collinearity (all GVIFs are smaller than 1.32). We tested specific hypotheses based on our a priori predictions and thus only the terms that represent these hypotheses were included and non-significant terms were retained in the models. We note that the inclusion of the non-significant terms did not influence the qualitative interpretation or significance of the other parameters.

Results

We observed 157 bird species in the study area (Appendix 2.1), of which 79 species (50.31%) mobbed in at least one of the experiments. Overall, 26 species mobbed both models, 50 species only mobbed the high-risk model (Ferruginous Pygmy-Owl), while three species only mobbed the low-risk model (Burrowing Owl).

Bird species with smaller body mass were more likely to mob (Table 2.1, Figure 2.1a). Species that forage in the understory or canopy were more likely to mob than species that forage on the ground (Table 2.1, Figure 2.1b).

Moreover, species that flock or live in stable groups were more likely to mob than solitary species (Table 2.2, Figure 2.1c). The social system did not influence whether species engaged in mobbing (Table 2.2). Also, the relative abundance of a species (encounter rate) did not influence whether it engaging in mobbing (Table 2.2).

Birds adjusted their mobbing behavior depending on the risk posed by a predator. The mobbing assemblage was larger when birds mobbed the high-risk predator model than the low-risk one (Table 2.2, Figure 2.2), but mobbing intensity and the mean body mass of species that mobbed did not influence the number of individuals in a mobbing assemblage (Table 2.2). Furthermore, birds mobbed more intensively when mobbing the model of a low-risk predator than the high-risk one (Figure 2.3), and individuals of smaller species mobbed more intensively than individuals of larger species (Table 2.3).

Table 2.1. Phylogenetically controlled generalized linear mixed model, using MCMCglmm, comparing the effect of body mass (logarithmic scale - g), foraging strata (ground, understory or canopy), flocking behavior (yes or no), and social organization (non-family/cooperative, family living, cooperative), the encounter frequency rate (encounter per min) on the propensity of species to mob or not mob predators. Significant P-values are highlighted in **bold**.

	estimate	95% CI		pMCMC
		lower	upper	
intercept	2.87	-0.73	6.02	0.11
body mass*	**-2.04**	**-2.75**	**-1.22**	**< 0.001**
foraging strata (ground vs. canopy) †	**3.40**	**0.87**	**5.83**	**< 0.001**
foraging strata (ground vs. understory) †	**2.66**	**0.46**	**4.96**	**0.010**
flocking behavior (no vs. yes) †	**1.83**	**0.58**	**3.00**	**0.006**
social organization (non-family vs. family) †	0.71	-0.79	1.93	0.30
social organization (non-family vs. coop.) †	1.08	-1.66	4.08	0.49
encounter frequency rate (encounter/min)	-11.15	-36.03	14.34	0.40
random effects				
phylogeny	1.03	0.74	1.30	

†Reference level is the first category in these lists.

Table 2.2. Phylogenetically controlled generalized linear mixed model, using MCMCglmm, comparing the effect of risk posed by a predator, mobbing intensity, season and body mass on the mobbing assemblage size. Significant P values are highlighted in **bold**.

	estimate	95% CI		pMCMC
		lower	upper	
intercept	**0.99**	**0.58**	**1.31**	**<0.001**
predator model (high-risk/low-risk)†	**0.35**	**0.04**	**0.68**	**0.034**
mobbing intensity	-0.00	-0.02	0.02	0.76
season (non-breeding/breeding)†	-0.15	-0.45	0.13	0.30
body mass	-0.00	-0.05	0.04	0.90
random effects				
phylogeny	0.005	0.001	0.01	
location	0.49	0.33	0.67	
date	0.03	0.00	0.09	

† Reference level is the first category in these lists.

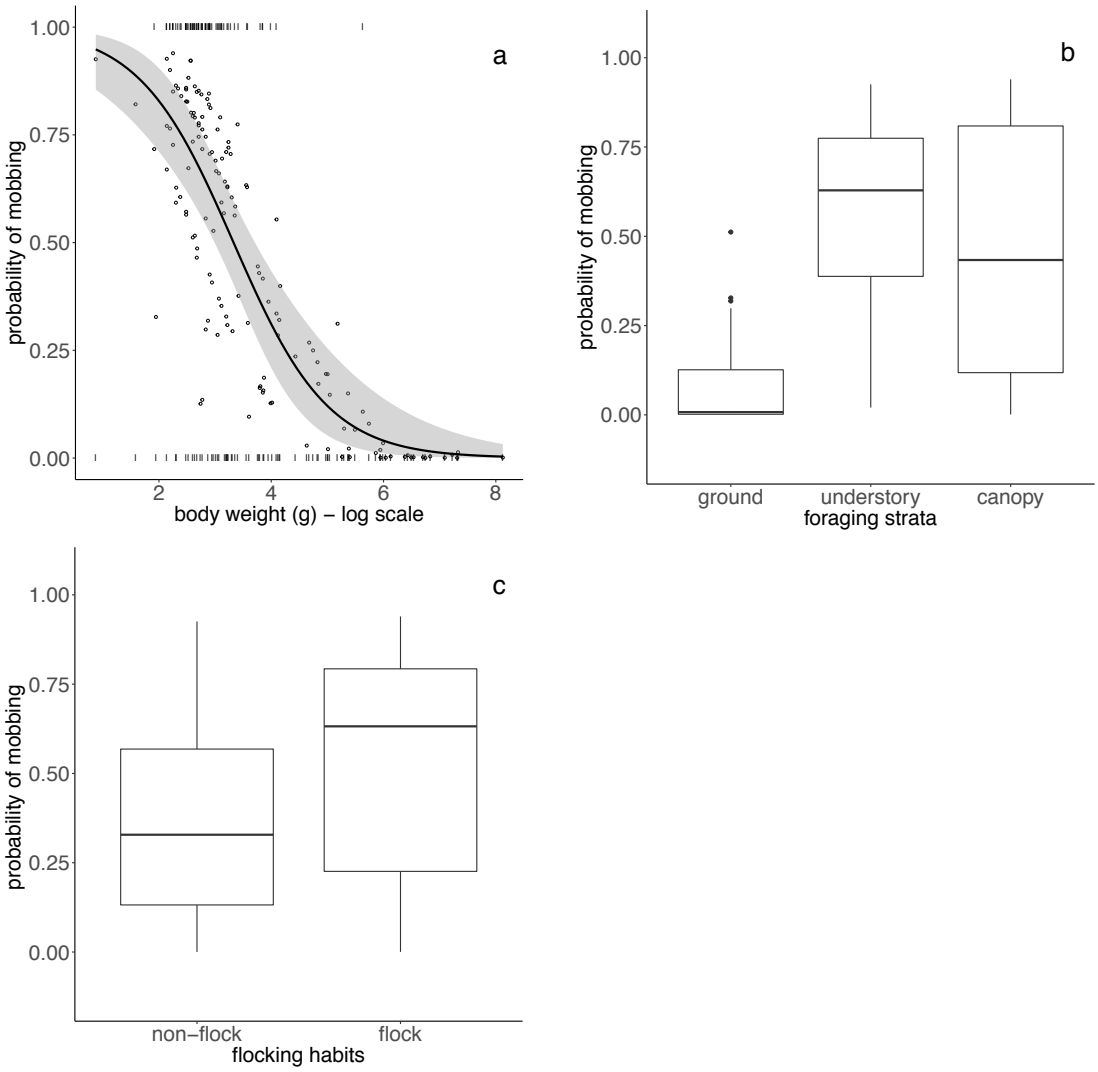

Figure 2.1. (a) Probability of species mob at least one of the two owl models according to the body mass of bird species. Graph based on predicted values from the generalized mixed model using MCMCglmm, the grey area indicates the 95% credible interval. The empty circles are the predict values, while the ticks are the raw values. (b) Probability of species mob at least one of the owl models according to the foraging strata that each species occupy. Graph based on predicted values from the generalized mixed model using MCMCglmm. (c) Probability of species mob at least one of the owl models according to the foraging strata that they occupy. Graph based on predicted values from the generalized mixed model using MCMCglmm.

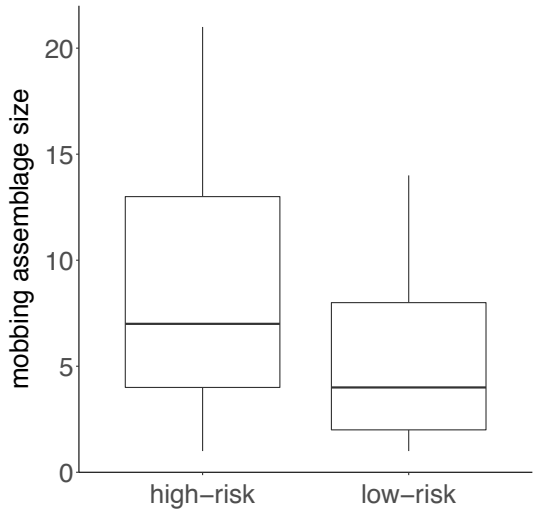

Figure 2.2. Number of individuals in the mobbing assemblage according to the risk represented by the predator stimuli (high-risk, low-risk). Graphs are based on raw data, bars indicate 95% confidence interval.

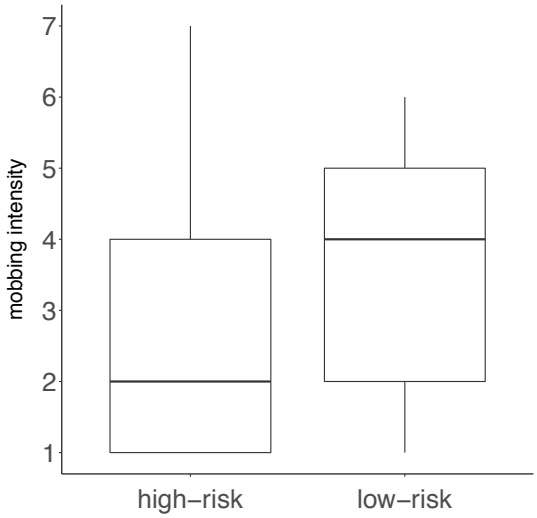

Figure 2.3. Mobbing intensity according to the risk represented by the predator stimuli (high-risk, low-risk). Graphs are based on raw data, bars indicate 95% confidence interval.

Table 2.3. Phylogenetically controlled generalized linear mixed model, using Markov chain Monte Carlo technique, comparing the effect of risk posed by a predator, mobbing assemblage size, season and body mass on the mobbing intensity. Significant P values are highlighted in **bold**.

	estimate	95% CI		pMCMC
		lower	upper	
intercept	**2.10**	**0.93**	**3.21**	**<0.001**
predator model (high-risk/low-risk)†	**-0.75**	**-1.39**	**-0.09**	**0.026**
mobbing assemblage	-0.01	-0.04	0.08	0.62
season (non-breeding/breeding)†	-0.08	-0.88	0.78	0.83
body mass	**-0.004**	**-0.008**	**-0.0006**	**0.032**
random effects				
phylogeny	1.00	0.97	1.02	
location	1.00	0.97	1.03	
date	0.99	0.97	1.02	

† Reference level is the first category in these lists.

Discussion

Our results revealed that particularly species that are potential prey engage in mobbing, but only if they can afford to do so. Accordingly, ground-living species that experience the highest risk of being killed by perch-hunting owls, and solitary species that cannot benefit from safety in numbers, were less likely to mob. In contrast, species that utilize safer parts of the habitat (understory or canopy), and species that benefit from safety in numbers, were more likely to engage in mobbing. Species that engaged in mobbing adjusted their behavior depending on the risk posed by the predator. In the presence of the high-risk predator, larger mobbing assemblages formed, but individuals took less risks than in the presence of a low-risk predator, confirming findings from previous studies (Maloney and McLean 1995; Veen et al. 2000; Griesser 2009).

Size matters hypothesis

It has been suggested that potential prey particularly mob predators (Hartley 1950; Dutour et al. 2016), but this hypothesis has so far not been tested across species. Our results lend support to this hypothesis, showing that species that engage in mobbing are lighter than species that do not mob, and thus, are within the prey body-size range of the two owl species (i.e., weigh less than 200g (Motta-Junior 2006; Carrera et al. 2008)).

Safer niche hypothesis

In support of this hypothesis, terrestrial species were less likely to mob than understory or canopy-living species. The owl models used in this study are perch-hunters that attack with a top-down strike, and consequently, terrestrial species are under the highest risk (Lima and Dill 1990; Kullberg and Ekman 2000; Hedenstrom 2001). Accordingly, they may have evolved alternative strategies of dealing with perched predators, for example by relying on camouflage as found in tinamous (Tinamidae) and nightjars (Caprimulgidae). The predation risk should not only vary depending on the strata, but also across different habitats. Since

our experiments were conducted in one habitat type only (i.e., relatively open areas at the edge of forest patches), we cannot test this hypothesis. A study on powerful owls *Ninox strenua* showed that they were equally likely to roost in forest patches and in open areas (Pavey and Smyth 1998). However, owls were more frequently mobbed in open habitats during daytime roosting (i.e., their typical hunting area at night), indicating that prey adjust their mobbing behavior depending on habitat-specific risks.

Safety in numbers hypothesis

A number of studies demonstrated that being in a larger group dilutes the risk to an individual (Hamilton 1971), and reduces the probability of a successful predator attack due to the confusion effect (Miller 1922). In support of this idea, our results showed that gregarious species that join flocks or live in stable groups are more likely to mob than solitary species (Table 2.1). Thus, even though solitary species could benefit from safety in numbers in a heterospecific mob, they still do not mob. This finding suggests that solitary species may have evolved different strategies of dealing with predators as discussed above, but further studies are required to explore this idea.

Social system hypothesis

Previous studies in a family-living bird species showed that parents mob more intensively in the presence of independent offspring (Griesser and Ekman 2005), and that mobbing provides a social learning opportunity to learn to recognize predators (Griesser and Suzuki 2017). In contrast to our prediction, the social system of a species did not influence their likelihood to engage in mobbing. Clearly, predator mobbing can have social functions also in non-family living species, such as providing opportunities to recruit partners for future mobbing events (Krams et al. 2008), to form dispersal coalitions (Maklakov 2002), or to display their quality to potential mates (Cunha et al. 2017).

Mobbing plasticity depending on the risk

Previous studies showed that birds recognize their predators (Curio et al. 1978b; Griesser and Ekman 2005), and adjust their behavior depending on the specific risks that a predator poses (Griesser 2009; Motta-Junior and Santos-Filho 2012; Tvardíková and Fuchs 2012). In accordance, our findings show that birds mob less intensely but form bigger assemblages when mobbing a high-risk predator compared to a low-risk predator. A previous study reported that Neotropical birds mobbed a dangerous predator (i.e., striped owl *Asio stygius*) more intensely than a less dangerous predator (i.e., barn owl *Tyto alba*) (Motta-Junior and Santos-Filho 2012). However, these species not only have very different diets, but they are also morphologically distinct and are crepuscular/nocturnal, which may influence the mobbing response of birds. In contrast, we used predator species that are morphologically similar and have diurnal habits. Diurnal owls are a constant threat to most diurnal bird species, therefore the risk of mob a potential threating predator at daytime may be higher than a nocturnal one, which does not impose an immediate threat. Thus, it may be less costly to approach high-risk nocturnal predator than a diurnal high-risk predators. Moreover, the similar plumage of the owls species excludes the possibility that differences in the mobbing behavior were caused by body coloration.

We did not find a difference in the mobbing behavior (intensity and assemblage size) across seasons (breeding vs. non-breeding). Similarly, a study with drongos (Dicrurus macrocercus and D. leucophaeus) showed that there was no difference in the frequency that birds mobbed their predators between different seasons (Nijman 2004). Birds may adjust their mobbing behavior according to the season particularly in a nest defense context (Shedd 1992; Shedd 193). We used predators of adults as stimuli, which pose a risk independent of the season. Moreover, some bird species are year-round territorial, and territoriality seems to influence aggressive behavior (Hau et al. 2004) and may also influence mobbing behavior, principally during the non-breeding season.

Conclusions

Animals can only die once, and thus, prey should adjust their behavior to minimize the risk of immediate death, for example during predator mobbing. Mobbing and other anti-predator behaviors generally are studied from the perspective of those that display it. However, to fully understand factors that facilitate the evolution of these behaviors, it is important to compare species that display these behaviors with those that do not display it. Our results show that only species that can afford mobbing, and do not pay too high costs, express this behavior. Clearly, mobbing is only beneficial for species that can be killed by a given predator.

Recent studies showed that predator mobbing also has important social functions, such as learning to recognize predators (Griesser and Suzuki 2017), to advertising their phenotypic quality to potential mates (Cunha et al. 2017), learning to recognize alarm calls of heterospecifics (Templeton and Greene 2007), and enhancing social bonds (Krams et al. 2008). Thus, mobbing can encompass a range of functions, calling for empirical studies that quantitatively assess the energetic costs and fitness benefits of mobbing across species, further contributing to the understanding of the evolution of risk taking behaviors.

APPENDIX CHAPTER TWO

Appendix 2.1

Below, the list of species registered in the study area (Table A1.2).

Table A1.2. List of all 157 bird species registered before and during the experiments in the study area.

Order	Family	Species	English Name
Accipitriformes	Accipitridae	Buteogallus meridionalis	Savanna Hawk
Accipitriformes	Accipitridae	Ictinia plumbea	Plumbeous Kite
Accipitriformes	Accipitridae	Buteo magnirostris	Roadside Hawk
Anseriformes	Anatidae	Amazonetta brasiliensis	Brazilian Teal
Anseriformes	Anatidae	Dendrocygna autumnalis	Black-bellied Whistling-Duck
Anseriformes	Anatidae	Dendrocygna viduata	White-faced Whistling-Duck
Apodiformes	Trochilidae	Amazilia fimbriata	Versicolored Emerald
Apodiformes	Trochilidae	Amazilia lactea	Sapphire-spangled Emerald
Apodiformes	Trochilidae	Chlorostilbon lucidus	Glittering-bellied Emerald
Apodiformes	Trochilidae	Colibri serrirostris	White-vented Violetear
Apodiformes	Trochilidae	Eupetomena macroura	Swallow-tailed Hummingbird
Apodiformes	Trochilidae	Heliomaster squamosus	Stripe-breasted Starthroat
Apodiformes	Trochilidae	Phaethornis pretrei	Planalto Hermit
Apodiformes	Trochilidae	Phaethornis ruber	Reddish Hermit
Cariamiformes	Cariamidae	Cariama cristata	Red-legged Seriema
Cathartiformes	Cathartidae	Coragyps atratus	Black Vulture
Cathartiformes	Cathartidae	Sarcoramphus papa	King Vulture
Charadriiformes	Recurvirostridae	Himantopus himantopus	White-backed Stilt
Charadriiformes	Jacanidae	Jacana jacana	Wattled Jacana
Charadriiformes	Charadriidae	Vanellus chilensis	Southern Lapwing
Columbiformes	Columbidae	Columbina picui	Picui Ground-Dove
Columbiformes	Columbidae	Columbina squammata	Scaled Dove
Columbiformes	Columbidae	Columbina talpacoti	Ruddy Ground-Dove
Columbiformes	Columbidae	Leptotila rufaxilla	Gray-fronted Dove
Columbiformes	Columbidae	Leptotila verreauxi	White-tipped Dove
Columbiformes	Columbidae	Patagioenas cayennensis	Pale-vented Pigeon
Columbiformes	Columbidae	Patagioenas picazuro	Picazuro Pigeon
Columbiformes	Columbidae	Patagioenas plumbea	Plumbeous Pigeon
Columbiformes	Columbidae	Zenaida auriculata	Eared Dove
Cuculiformes	Cuculidae	Coccyzus americanus	Yellow-billed Cuckoo
Cuculiformes	Cuculidae	Crotophaga ani	Smooth-billed Ani
Cuculiformes	Cuculidae	Guira guira	Guira Cuckoo
Cuculiformes	Cuculidae	Piaya cayana	Squirrel Cuckoo
Cuculiformes	Cuculidae	Tapera naevia	Striped Cuckoo

Order	Family	Species	English Name
Falconiformes	Falconidae	Caracara plancus	Southern Caracara
Falconiformes	Falconidae	Falco femoralis	Aplomado Falcon
Falconiformes	Falconidae	Herpetotheres cachinnans	Laughing Falcon
Galbuliformes	Galbulidae	Galbula ruficauda	Rufous-tailed Jacamar
Gruiformes	Rallidae	Gallinula chloropus	Common Gallinule
Passeriformes	Furnariidae	Phacellodomus ruber	White-collared Foliage-gleaner
Passeriformes	Motacillidae	Anthus lutescens	Yellowish Pipit
Passeriformes	Pipridae	Antilophia galeata	Helmeted Manakin
Passeriformes	Passerellidae	Arremon flavirostris	Saffron-billed Sparrow
Passeriformes	Tyrannidae	Camptostoma obsoletum	Southern Beardless-Tyrannulet
Passeriformes	Troglodytidae	Thryothorus leucotis	Buff-breasted Wren
Passeriformes	Tyrannidae	Casiornis rufus	Rufous Casiornis
Passeriformes	Icteridae	Chrysomus ruficapillus	Chestnut-capped Blackbird
Passeriformes	Tyrannidae	Cnemotriccus fuscatus	Fuscous Flycatcher
Passeriformes	Thraupidae	Coereba flaveola	Bananaquit
Passeriformes	Tyrannidae	Colonia colonus	Long-tailed Tyrant
Passeriformes	Thraupidae	Conirostrum speciosum	Chestnut-vented Conebill
Passeriformes	Conopophagidae	Conopophaga lineata	Rufous Gnateater
Passeriformes	Thraupidae	Coryphospingus pileatus	Pileated Finch
Passeriformes	Rhynchocyclidae	Corythopis delalandi	Southern Antpipit
Passeriformes	Corvidae	Cyanocorax cristatellus	Curl-crested Jay
Passeriformes	Vireonidae	Cyclarhis gujanensis	Rufous-browed Peppershrike
Passeriformes	Thraupidae	Dacnis cayana	Blue Dacnis
Passeriformes	Thamnophilidae	Dysithamnus mentalis	Plain Antvireo
Passeriformes	Tyrannidae	Elaenia chiriquensis	Lesser Elaenia
Passeriformes	Tyrannidae	Elaenia cristata	Plain-crested Elaenia
Passeriformes	Tyrannidae	Elaenia flavogaster	Yellow-bellied Elaenia
Passeriformes	Tyrannidae	Empidonomus varius	Variegated Flycatcher
Passeriformes	Thraupidae	Eucometis penicillata	Gray-headed Tanager
Passeriformes	Fringillidae	Euphonia chlorotica	Purple-throated Euphonia
Passeriformes	Tyrannidae	Euscarthmus meloryphus	Tawny-crowned Pygmy-Tyrant
Passeriformes	Tyrannidae	Fluvicola nengeta	Masked Water-Tyrant
Passeriformes	Furnariidae	Furnarius rufus	Rufous Hornero
Passeriformes	Icteridae	Gnorimopsar chopi	Chopi Blackbird
Passeriformes	Rhynchocyclidae	Hemitriccus margaritaceiventer	Pearly-vented Tody-tyrant
Passeriformes	Thamnophilidae	Herpsilochmus atricapillus	Black-capped Antwren
Passeriformes	Tyrannidae	Hirundinea ferruginea	Cliff Flycatcher
Passeriformes	Vireonidae	Hylophilus poicilotis	Rufous-crowned Greenlet
Passeriformes	Pipridae	Ilicura militaris	Pin-tailed Manakin
Passeriformes	Tyrannidae	Lathrotriccus euleri	Euler's Flycatcher
Passeriformes	Tyrannidae	Legatus leucophaius	Piratic Flycatcher
Passeriformes	Tyrannidae	Megarynchus pitangua	Boat-billed Flycatcher
Passeriformes	Mimidae	Mimus saturninus	Chalk-browed Mockingbird
Passeriformes	Rhynchocyclidae	Mionectes rufiventris	Gray-hooded Flycatcher
Passeriformes	Tyrannidae	Myiarchus ferox	Short-crested Flycatcher

Order	Family	Species	English Name
Passeriformes	Tyrannidae	Myiarchus swainsoni	Swainson's Flycatcher
Passeriformes	Tyrannidae	Myiarchus tyrannulus	Brown-crested Flycatcher
Passeriformes	Tyrannidae	Myiodynastes maculatus	Streaked Flycatcher
Passeriformes	Tyrannidae	Myiopagis caniceps	Gray Elaenia
Passeriformes	Tyrannidae	Myiopagis viridicata	Greenish Elaenia
Passeriformes	Tyrannidae	Myiophobus fasciatus	Bran-colored Flycatcher
Passeriformes	Parulidae	Basileuterus flaveolus	Flavescent Warbler
Passeriformes	Tyrannidae	Myiozetetes cayanensis	Rusty-margined Flycatcher
Passeriformes	Tyrannidae	Myiozetetes similis	Social Flycatcher
Passeriformes	Thraupidae	Nemosia pileata	Hooded Tanager
Passeriformes	Pipridae	Neopelma pallescens	Pale-bellied Tyrant-Manakin
Passeriformes	Tityridae	Pachyramphus polychopterus	White-winged Becard
Passeriformes	Furnariidae	Phacellodomus ferrugineigula	Orange-breasted Thornbird
Passeriformes	Furnariidae	Phacellodomus rufifrons	Rufous-fronted Thornbird
Passeriformes	Tyrannidae	Phaeomyias murina	Mouse-colored Tyrannulet
Passeriformes	Tyrannidae	Pitangus sulphuratus	Great Kiskadee
Passeriformes	Platyrinchidae	Platyrinchus mystaceus	White-throated Spadebill
Passeriformes	Hirundinidae	Progne tapera	Brown-chested Martin
Passeriformes	Icteridae	Psarocolius decumanus	Crested Oropendola
Passeriformes	Hirundinidae	Pygochelidon cyanoleuca	Blue-and-white Swallow
Passeriformes	Thraupidae	Saltator similis	Green-winged Saltator
Passeriformes	Parulidae	Parula pitiayumi	Tropical Parula
Passeriformes	Thraupidae	Sicalis flaveola	Saffron Finch
Passeriformes	Dendrocolaptidae	Sittasomus griseicapillus	Olivaceous Woodcreeper
Passeriformes	Thraupidae	Sporophila nigricollis	Yellow-bellied Seedeater
Passeriformes	Hirundinidae	Stelgidopteryx ruficollis	Southern Rough-winged Swallow
Passeriformes	Furnariidae	Synallaxis albescens	Pale-breasted Spinetail
Passeriformes	Furnariidae	Synallaxis frontalis	Sooty-fronted Spinetail
Passeriformes	Furnariidae	Synallaxis spixi	Spix's Spinetail
Passeriformes	Thraupidae	Thraupis palmarum	Palm Tanager
Passeriformes	Thraupidae	Thraupis sayaca	Sayaca Tanager
Passeriformes	Thamnophilidae	Taraba major	Great Antshrike
Passeriformes	Thraupidae	Tersina viridis	Swallow Tanager
Passeriformes	Thamnophilidae	Thamnophilus caerulescens	Variable Antshrike
Passeriformes	Thamnophilidae	Thamnophilus doliatus	Barred Antshrike
Passeriformes	Thamnophilidae	Thamnophilus torquatus	Rufous-winged Antshrike
Passeriformes	Tyrannidae	Todirostrum poliocephalum	Yellow-lored Tody-Flycatcher
Passeriformes	Rhynchocyclidae	Tolmomyias sulphurescens	Yellow-olive Flycatcher
Passeriformes	Troglodytidae	Troglodytes aedon	House Wren
Passeriformes	Turdidae	Turdus amaurochalinus	Creamy-bellied Thrush
Passeriformes	Turdidae	Turdus leucomelas	Pale-breasted Thrush
Passeriformes	Turdidae	Turdus rufiventris	Rufous-bellied Thrush
Passeriformes	Tyrannidae	Tyrannus melancholicus	Tropical Kingbird
Passeriformes	Thraupidae	Volatinia jacarina	Blue-black Grassquit
Passeriformes	Tyrannidae	Xolmis cinereus	Gray Monjita

Order	Family	Species	English Name
Passeriformes	Passerellidae	Zonotrichia capensis	Rufous-collared Sparrow
Pelecaniformes	Ardeidae	Casmerodius albus	Great Egret
Pelecaniformes	Ardeidae	Egretta thula	Snowy Egret
Pelecaniformes	Ardeidae	Nycticorax nycticorax	Black-crowned Night-Heron
Pelecaniformes	Ardeidae	Syrigma sibilatrix	Whistling Heron
Piciformes	Picidae	Campephilus melanoleucos	Crimson-crested Woodpecker
Piciformes	Picidae	Colaptes campestris	Campo Flicker
Piciformes	Picidae	Colaptes melanochloros	Green-barred Woodpecker
Piciformes	Picidae	Dryocopus lineatus	Lineated Woodpecker
Piciformes	Picidae	Melanerpes candidus	White Woodpecker
Piciformes	Ramphastidae	Ramphastos toco	Toco Toucan
Piciformes	Picidae	Veniliornis passerinus	Little Woodpecker
Psittaciformes	Psittacidae	Amazona aestiva	Turquoise-fronted Parrot
Psittaciformes	Psittacidae	Brotogeris chiriri	Yellow-chevroned Parakeet
Psittaciformes	Psittacidae	Aratinga aurea	Peach-fronted Parakeet
Psittaciformes	Psittacidae	Forpus xanthopterygius	Blue-winged Parrotlet
Strigiformes	Strigidae	Glaucidium brasilianum	Ferruginous Pygmy-Owl
Tinamiformes	Tinamidae	Crypturellus obsoletus	Brown Tinamou
Tinamiformes	Tinamidae	Crypturellus parvirostris	Small-billed Tinamou
Tinamiformes	Tinamidae	Crypturellus tataupa	Tataupa Tinamou
Tinamiformes	Tinamidae	Rhynchotus rufescens	Red-winged Tinamou

Appendix 2.2

Variance Inflation Factor

We checked the collinearity and possible relations among the main effects of our Generalised Linear Mixed Models by analysing the generalized variance inflation factor (GVIF) using the package 'car' (Fox and Weisberg 2011). Overall the GVIF values were no bigger than 2.6 (Tables A2.2, A3.2, A4.2). In this way we conclude that the collinearity effect among the main factors could be ignored.

Table A2.2. Generalised Variance Inflation Factors' values for the main effects included in Generalised Linear Mixed Model using Markov chain Monte Carlo technique. This values were obtained using the package 'car' (Fox and Weisberg 2011) in R software (R Core Team 2015)

	main effects				
	body weight (log scale)	foraging strata	flocking behavior	family system	encounter rate
GVIF values	1.310	1.140	1.192	1.276	1.310

Table A3.2. Variance Inflation Factors' values for the main effects included in Generalised Linear Mixed Model using Markov chain Monte Carlo technique. This values were obtained using the package 'car' (Fox and Weisberg 2011) in R software (R Core Team 2015)

	main effects			
	body weight	maximum mobbing intensity rank	predator model (low-risk and high-risk)	season (breeding and non-breeding)
GVIF values	1.024	1.087	1.008	1.024

Table A4.2. Variance Inflation Factors' values for the main effects included in Generalised Linear Mixed Model using Markov chain Monte Carlo technique. This values were obtained using the package 'car' (Fox and Weisberg 2011) in R software (R Core Team 2015)

	main effects			
	body weight	mobbing assemblage size	predator model (low-risk and high-risk)	season (breeding and non-breeding)
GVIF values	1.005	1.165	1.040	1.127

CHAPTER THREE

The presence of conspecific females influences male mobbing behavior

Filipe C.R. Cunha[1,2], Julio C.R. Fontenelle[3] and Michael Griesser[1]

Many prey species mob predators to drive them away, thereby reducing their immediate and future predation risk. Given that mobbing is risky, it may also serve as an opportunity for males to advertise their phenotypic quality to females, however this idea remains untested. We tested this hypothesis with a field experiment in south-eastern Brazil that assessed the response of sexually dimorphic bird species to models of two diurnal owls: a Ferruginous Pygmy-owl (*Glaucidium brasilianum*), which mainly eats small birds, and a Burrowing Owl (*Athene cunicularia*), which mainly eats invertebrates and thus poses a low risk to birds. Across 19 bird species, the mobbing intensity was higher when facing the less-dangerous owl, and more males engaged in predator mobbing than females. The mobbing intensity of males was higher with a larger number of conspecific females present. This finding indicates that males may use mobbing to display their phenotypic quality to females, suggesting that predator mobbing may be influenced by sexual selection.

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Introduction

Predation is a key cause of mortality in many species, and accordingly, prey species have evolved a number of anti-predatory defenses, such as mimicry, camouflage, predator mobbing or feigning death (Caro 2005). Prey should benefit from adjusting their responses according to the risk posed by the predator. Indeed, field studies have shown that birds behave differently in response to different predators depending on the risk they pose (Griesser 2009; Motta-Junior and Santos-Filho 2012).

Mobbing is a widespread anti-predatory behavior, which consists of a prey approaching a potential predator to harass it by giving calls, swooping over it, or even physically attacking it. While mobbing is costly (Dugatkin and Godin 1992; Krama and Krams 2005) and potentially lethal (Sordahl 1990), it has been suggested to be adaptive (Curio et al. 1978a). Predators often move away when being mobbed, reducing the immediate and future risk of an attack (Pavey and Smyth 1998). In addition, predator mobbing may serve as an opportunity to receive support during future predator mobbing events (Krams et al. 2008), or as a social learning opportunity for juveniles (Griesser and Suzuki 2016) to learn to recognize predators (Griesser and Suzuki 2017).

Moreover, mobbing may serve as a costly signal (Maklakov 2002) of phenotypic quality to conspecifics (Arnold 2000), especially potential mates (Curio et al. 1983; Regelmann and Curio 1986). In many species, males are generally more aggressive than females (Francis et al. 1989; Bard et al. 2002), and mob predators more vigorously than females (Curio et al. 1983; Maklakov 2002; Griesser and Ekman 2005). However, it remains unclear why males and females differ in their mobbing behavior, and whether this behavior may be influenced by sexual selection.

Here we investigate whether the presence of females influences the mobbing intensity of males in 19 bird species. We exposed birds to two sympatric owl species that vary in their risk to birds, and measured the size of the mobbing assembly and the mobbing intensity of all individuals that joined the mobbing assembly. We tested the following two non-exclusive hypotheses: i) if birds recognize the risk posed by a predator, and mobbing aims at reducing the immediate risk, the birds will mob a dangerous predator more intensely than a low-risk predator; ii) if mobbing is a sexually selected

behavior, males will mob more intensely when more conspecific females are present, using it as an opportunity to advertise their phenotypic quality.

Material and Methods

Study site

This study was conducted on Cauaia Ranch, Minas Gerais State, South-eastern Brazil (19°28`S 44°01`W) between February 2011 and February 2012, encompassing both the breeding season (October to March) and the non-breeding season (April to September). The landscape at the study site is dominated by a mosaic of semi-deciduous forests, Brazilian savannah areas and agricultural fields. All the experiments were conducted in the edge of forest patches with sparse tree and bushes, providing perches to birds during mobbing but allowing good visibility of birds in all directions for at least 20 m.

Experimental procedure

We selected 18 locations that were at least 250 m apart to minimize the risk of resampling the same individuals on the same day (Bibby et al. 2012). Within each location, we placed the model on a 1.5 m pole, 2 m away from an approximately 3 m high tree. We used two models of owl species that are similar in their coloration and size but differ in their risk to birds: a Ferruginous Pygmy-owl model (*Glaucidium brasilianum*, body length = 16.8 cm; 43% of its diet consists of birds (Carrera et al. 2008)), and a Burrowing Owl model (*Athene cunicularia*, body length = 22.4 cm; 95% of its diet consists of arthropods (Zilio 2006) but it occasionally eats birds (Motta-Junior 2006)). An earlier study showed that the size of predators may affect the mobbing intensity of birds (Templeton et al. 2005). Thus, using similarly sized species controls for the influence of body size on mobbing intensity.

We performed 96 experiments with each model throughout the year (5-6 experiments in each location per model). The order of the experiments in each location followed a Latin square design, and we randomly chose different experimental sites within each location. To attract birds to the model and simulate the presence of a live predator, we placed a speaker below the model and played-back vocalizations of the respective predator species (calling bouts of 30 sec followed by 15 sec silence). The observer was positioned 10-15 m from the model wearing camouflage clothes. We registered the

behaviors of all present individuals and their distance to the predator during 10 min with a voice recorder. It was not possible to record data blind because our study involved observation of wild animals in the field.

We assessed the maximum mobbing intensity for each bird that mobbed the models during the experiment using a scale of mobbing intensity from 1-7 (following Chandler and Rose 1988; Motta-Junior and Santos-Filho 2012): 1) an individual was > 10m away from model making visual displays, emitting warning calls or being silent, 2) an individual was ≤ 10m and > 5m away making visual displays, emitting warning calls or being silent, 3) an individual was ≤ 5m and > 2m away and being silent, 4) an individual was ≤ 5m and > 2m away making visual displays and/or giving warning calls, 5) an individual was ≤ 2m away and being silent, 6) an individual was ≤ 2m away making visual displays and/or giving warning calls but not attacking the model and 7) an individual was physically attacking the model. Distances between the birds and the model were assessed with the help of distance marks in trees placed in the four main cardinal directions (north, south, east and west) before the experiment.

In total, 79 different bird species mobbed the models, but we included only 19 species that have conspicuous sexual color dimorphism to assess the response variable in our analyses (Table 3.1), allowing unambiguous discrimination of females and males in the field. These species belong to six different taxonomic groups which are mostly poorly studied but display a large variety of mating, parental care and social systems (del Hoyo et al. 2015). Trochilidae (hummingbirds) are typically polygynyous and females alone care for the brood. Galbulidae (jacamars) usually have biparental brood care and males engage in courtship feeding. Picidae (woodpeckers) have biparental brood care and live solitarily, in couples or in small family groups. Thamnophilidae (antbirds) usually have biparental brood care and are family group-living. Tyrannidae (tyrant flycatchers) are presumably monogamous, pair-bonded, and have biparental brood care. Thraupidae (tanagers) usually have biparental brood care and extra-pair paternity is common, and are frequently part of mixed flocks or large groups. The specific breeding and social systems have not been studied in the study populations, and thus were not considered here. However, given that female choice is predominant in birds (Searcy 1979; Majerus 1986) it is expected that

males use any opportunity to advertise their phenotypic qualities to their current mate, future mates or potential extra-pair mating partners.

Table 3.1. Color-dimorphic species included in this study. Taxonomy follows (Jetz et al. 2012)

Taxonomic family	Scientific name	English Name
Trochilidae	*Colibri serrirostris*	White-vented Violetear
	Chlorostilbon lucidus	Glittering-bellied Emerald
	Heliomaster squamosus	Stripe-breasted Starthroat
Galbulidae	*Galbula ruficauda*	Rufous-tailed Jacamar
Picidae	*Picumnus cirratus*	White-barred Piculet
	Veniliornis passerinus	Little Woodpecker
	Campephilus melanoleucos	Crimson-crested Woodpecker
Thamnophilidae	*Herpsilochmus atricapillus*	Black-capped Antwren
Tyrannidae	*Colonia colonus*	Long-tailed Tyrant
Thraupidae	*Nemosia pileata*	Hooded Tanager
	Lanio pileatus	Pileated Finch
	Tangara cayana	Burnished-buff Tanager
	Tersina viridis	Swallow Tanager
	Dacnis cayana	Blue Dacnis
	Hemithraupis ruficapilla	Rufous-headed Tanager
	Volatinia jacarina	Blue-black Grassquit
	Sporophila nigricollis	Yellow-bellied Seedeater
	Euphonia chlorotica	Purple-throated Euphonia

Statistical analyses

We used the software R for our analyses (R Core Team 2015). To test the influence of the presence of female and male conspecifics on the maximum mobbing intensity of each individual in the mobbing assemblage, we used a Generalized Linear Mixed Model using Markov chain Monte Carlo techniques in the package MCMCglmm (Hadfield 2010). We used the maximum mobbing intensity as our response variable and included the following predictors: predator model (high-risk or low-risk), interaction between the sex of the individual and the total number of conspecific females in the mobbing assemblage, interaction between the sex of the individual and the number of conspecific males in the mobbing assemblage, interaction between the sex of the individual and the number of total individuals in the mobbing assemblage (conspecifics and heterospecifcs), and season (breeding or non-breeding). Given that we tested specific hypothesis based on a priori predictions, all non-significant terms were retained in the models. We included a consensus tree of a recent phyla-wide phylogeny (Jetz et al. 2012) and the location of each experiment as random factors to control for species-specific differences in their abundance

and mobbing behavior, and to control for potential non-independency of the data, since individuals were not marked. The MCMCglmm model resulted in balanced trace-plots and an effective sample size of around 1000 for all variables. We checked the model convergence by analyzing the trace plots, the residuals and the predicted values of the model. We checked for collinearity among the main effects through the variance inflation factor using the package 'car' (Fox and Weisberg 2011). All values were < 2.2, showing that collinearity among the main effects was negligible (Appendix 3.1).

An ordinal regression model with phylogenetic control was not practicable, due to quasi-separation of the data (i.e., some clades were only represented by a single rank). Therefore, maximum mobbing intensity was analyzed using a linear mixed model. An earlier simulation study showed that ordinal variables with more than five levels can be reasonably assessed using approaches designed for continuous data (Rhemtulla et al. 2012). We note that an ordinal regression in a generalized linear mixed model without phylogenetic control yields qualitatively similar results (Appendix 3.2).

Results

We observed at least one individual of a sexually dimorphic species in 54 experiments. Overall, 165 individuals of 19 sexually dimorphic species approached the predator models (mean number of total individuals - sexually dimorphic and non sexually dimorphic - per experiment = 13.09, ranging from 1 to 21). The majority of the individuals that mobbed were males (n=108), independent of the predator species. While 126 individuals mobbed the high-risk model, only 39 individuals mobbed the low-risk model. More males mobbed when exposed to both the high-risk predator model (82 males, 44 females) and the low-risk predator model (26 males, 13 females). In most experiments no conspecific individuals were present in the mobbing assemblage, independent of the sex of the mobber (Table 3.2). The number of conspecific females varied between 0 and 3 (mean = 1.53), while the number of conspecific males varied between 0 and 7 (mean = 2.27).

Overall, birds mobbed a low-risk predator model more intensively than a high-risk predator model (Figure 3.1, Table 3.3), but males and females did not differ in their mobbing intensity (Table 3.3). We did not find a difference in mobbing intensity between the breeding and non-breeding season (Table 3.3). Total mobbing assemblage size

(counting conspecific and heterospecific individuals) did not influence the mobbing behavior of either sex (Table 3.3). However, the composition of the audience influenced the mobbing behavior of males. They mobbed more intensely when more conspecific females were present (Figure 3.2; Table 3.3), but the number of males had no influence (Table 3.3). The mobbing behavior of females did not depend on the audience size or composition (Table 3.3).

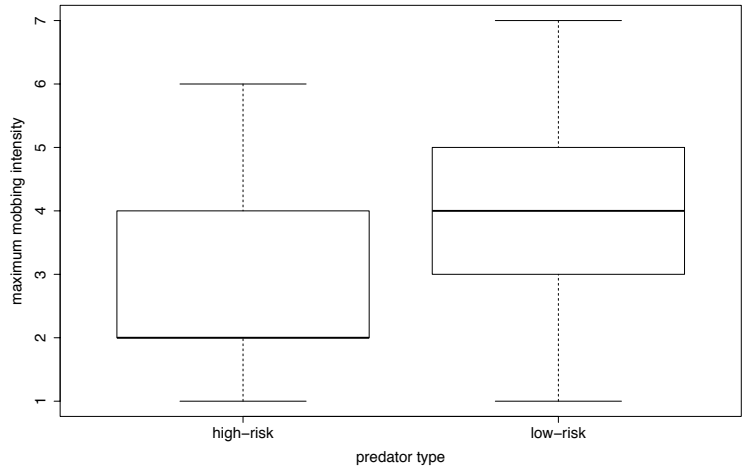

Figure 3.1. Mobbing intensity according to the predator stimuli. Boxplots show the median, maximum and minimum mobbing intensity per treatment.

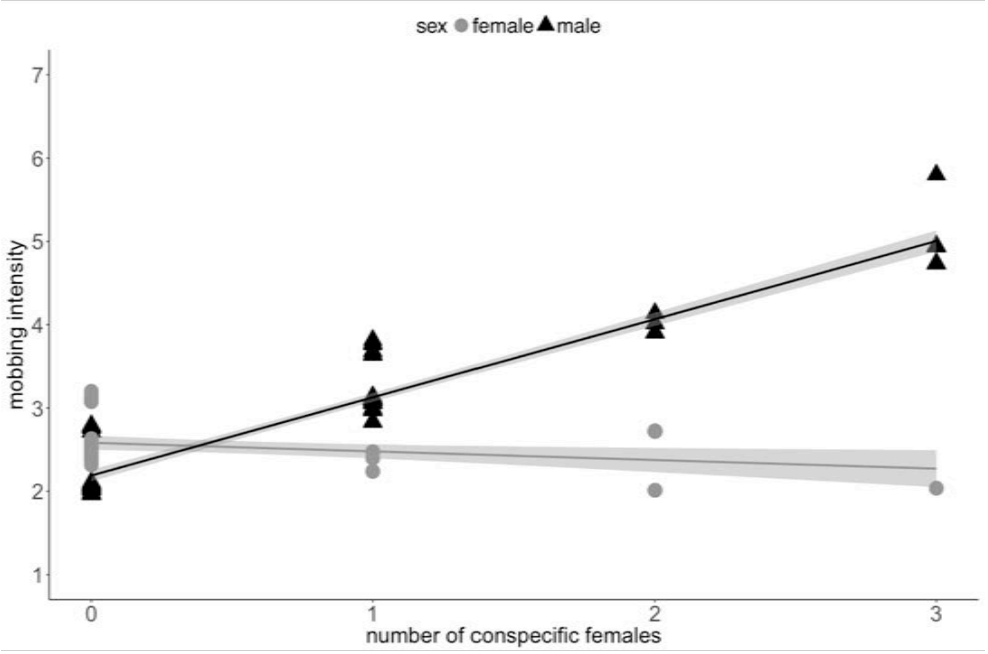

Figure 3.2 Mobbing intensity of females and males in relation to the number of conspecific females in the mobbing assemblage based on the predicted values from the model. Grey areas represent the 95% credible interval.

Table 3.2. Frequency of additional conspecific males and females in mobbing assemblages. The column on the right indicates the sex of the sampled individual. The table is divided by the frequency of additional males (upper part) and the frequency of additional females (lower part)

Number of additional conspecific females in the mobbing assemblage	Number of additional conspecific males in the mobbing assemblage						
	0	**1**	**2**	**3**	**4**	**7**	
0	38	9	0	0	0	0	♂
1	27	12	3	0	0	0	
2	1	2	3	0	0	0	
3	1	0	0	4	8	8	
	0	**1**	**2**	**3**	**4**	**8**	
0	7	28	5	1	0	0	♀
1	1	2	2	0	0	0	
2	0	3	0	0	3	3	
3	0	2	0	0	0	0	

Table 3.3. Influence of the predator model, sex of the mobber (males or female), the presence of conspecific (females or males), the total number of individuals in the mobbing assemblage (conspecifics and heterospecifics) and season (non-breeding or breeding) on the mobbing intensity of females and males. Significant p values are highlighted in **bold**.

	estimate	95% CI		pMCMC
		lower	upper	
Intercept	**2.56**	**1.02**	**3.89**	**0.004**
sex (female vs. male) †	-0.06	-1.16	1.00	0.89
number of conspecific females in the mobbing assemblage	-0.14	-0.77	0.42	0.63
number of conspecific males in the mobbing assemblage	-0.06	-0.36	0.24	0.67
total number of individuals in the mobbing assemblage	0.01	-0.06	0.09	0.74
predator model (high-risk vs. low-risk)	**0.95**	**0.24**	**1.63**	**0.014**
season (non-breeding vs. breeding) †	-0.13	-0.84	0.45	0.65
sex (female vs. male) † x number of conspecific females in the mobbing assemblage	**1.13**	**0.28**	**1.88**	**0.009**
sex (female vs. male) † x number of conspecific males in the mobbing assemblage	-0.09	-0.48	0.30	0.66
sex (female vs. male) † x total mobbing assemblage	-0.03	-0.11	0.07	0.48
random effects				
phylogeny	0.957	0.003	2.84	
location	0.068	0.002	0.23	

† Reference level is the first category in these lists

Discussion

Mobbing is an anti-predatory behavior that primarily aims at moving the predator away, reducing both the immediate and future predation risk (Pavey and Smyth 1998). Since mobbing is risky (Sordahl 1990), it may also serve as an honest signal of phenotypic quality (Zahavi and Zahavi 1997), giving males the opportunity to display their quality to potential mates. Our results support this hypothesis, by showing that male birds mob more intensively in the presence of more conspecific females, but not in the presence of more conspecific males.

This pattern could reflect two different processes: males may increase their mobbing intensity after more females join a mobbing assemblage, or more conspecific females may join the assemblage due to high male mobbing intensity. However, it is difficult to assess when males perceive the presence of females in the field, which would be critical to understand which of the two processes occurs. Regardless of the order of events, our data show that the mobbing intensity was not related to assemblage size but only to the number of conspecific females, which suggests that mobbing is influenced by sexual selection. This novel finding highlights the general importance of sexual selection, and may help to better understand the evolution of anti-predatory behaviors.

It is well known that birds recognize the specific risks predators pose (Curio et al. 1978b; Griesser 2008). In contrast to our prediction, our experiments showed that birds mob a low-risk predator more intensively than a high-risk one, supporting findings from previous studies (Forsman and Mönkkönen 2001; Griesser and Ekman 2005; Griesser 2009). Thus, despite that driving away a high-risk predator is more beneficial, mobbing it is riskier, suggesting that immediate costs influence mobbing intensity.

In a wide range of species, males show more aggression than females (Bard et al. 2002). Our experiment confirms that males were more likely to mob predators (Maklakov 2002; Griesser and Ekman 2005), yet males were sensitive to the number of conspecific females in the mobbing assemblage. Earlier studies showed that males can be sensitive to their audience, adjusting sexual displays depending on the number and/or the quality of (potential) partners (Matos and McGregor 2002; Dubois and Belzile 2012). Clearly, it would be interesting to assess in future experiments whether an increased mobbing effort actually results in a higher mating success for males. If mobbing is costly signaling, and

therefore sexually selected, we would expect that the audience effect would be higher in polygamous species than in monogamous species (Kirkpatrick et al. 1990). Since the mating and parental care systems for the birds in our study population are not studied, we could not assess their influence on the mobbing intensity of males.

Experiments in chaffinches Fringilla coelebs showed that males increased their predator mobbing effort during the first weeks of the breeding season (Krams and Krama 2002). This result was suggested to reflect interspecific reciprocity, but it may also reflect a benefit of advertising quality to neighbor females (to gain access to extra-pair mating opportunities) or to neighbor males (as a consequence of male-male competition). Similarly, male great tits Parus major mob predators more intensely than females (Curio et al. 1983), which may reflect that males are using mobbing to advertise phenotypic qualities. Thus, mobbing could be a sexually selected signal in other species but more experiments are needed to validate the generality of this hypothesis.

Several other factors may influence differences in mobbing behavior in general and between sexes. Temperate birds have been shown to mob more intensely during the breeding season (Shedd 1983), especially when a predator is close to their nest (Kryštofková et al. 2011). Accordingly, the breeding status can influence the mobbing intensity of males and females across species. However, we did not find a significant difference in mobbing intensity between the breeding and non-breeding season. This result may reflect that tropical and temperate birds differ in their response to nest predators, or that the species included in this study breed in different micro-habitats that the ones we chose for our experiment. Furthermore, the mating status of males could influence their mobbing effort, which would be interesting to address in future studies.

To conclude, our results suggest that males across 19 species can use mobbing as an opportunity to display their phenotypic quality to females, highlighting the ubiquitous importance of sexual selection (Andersson 1994). Female choice can be influenced by the motor skills of males, which provides clues about their ability to defend a nest or forage successfully (Barske et al. 2011). Since mobbing a predator is risky, only males with good motor skills that are capable of swiftly escaping can afford to approach a predator, making predator mobbing a potentially honest signal of phenotypic quality (Zahavi and Zahavi1997).

APPENDIX CHAPTER THREE

Appendix 3.1

Variance Inflation Factor

We checked the collinearity and possible relations among the main effects of our Generalised Linear Mixed Model using Markov chain Monte Carlo technique analysing the variance inflation factor using the package 'car' (Fox and Weisberg 2011), all the values were no bigger than 2.2 (Table A1.3). In this way we conclude that there was no collinearity among the main effects.

Table A1.3 Variance Inflation Factors' values for the main effects included in Generalised Linear Mixed Model using Markov chain Monte Carlo technique. This values were obtained using the package 'car' (Fox and Weisberg 2011) in R software (R Core Team 2016)

	main effects					
	sex	number of conspecific females in the mobbing assemblage	number of conspecific males in the mobbing assemblage	total number of birds in the mobbing assemblage	predator model (low-risk and high-risk)	season (breeding and non-breeding)
VIF values	1.181	1.935	2.142	1.377	1.267	1.334

Model without phylogenetic control

As the mobbing intensity fits an ordinal scale we present a model in which mobbing intensity is treated as an ordinal variable (Table A2.3). This model, however does not include phylogeny as random effect. Nevertheless, the results remain qualitatively the same as the ones obtained by a linear model (Table 3.3).

Table A2.3. Influence of the predator model, sex of the mobber (males or female), the presence of conspecific (females or males), the total number of individuals in the mobbing assemblage (conspecifics and heterospecifics) and season (non-breeding or breeding) on the mobbing intensity of females and males. Significant p values are highlighted in **bold**

	estimate	95% CI		pMCMC
		lower	upper	
Intercept	**1.003**	**0.069**	**1.878**	**0.021**
sex (female vs. male) †	-0.294	-1.264	0.702	0.528
number of conspecific females in the mobbing assemblage	-0.129	-0.649	0.382	0.635
number of conspecific males in the mobbing assemblage	-0.009	-0.280	0.237	0.949
total number of individuals in the mobbing assemblage	0.014	-0.057	0.077	0.672
predator model (high-risk vs. low-risk)	**0.703**	**0.072**	**1.296**	**0.027**
season (non-breeding vs. breeding) †	0.037	-0.502	0.579	0.923
sex (female vs. male) † x number of conspecific females in the mobbing assemblage	**1.146**	**0.384**	**1.815**	**<0.001**
sex (female vs. male) † x number of conspecific males in the mobbing assemblage	-0.070	-0.434	0.256	0.678
sex (female vs. male) † x total mobbing assemblage	-0.018	-0.099	0.061	0.650
random effects				
location	0.019	<0.001	0.053	

CHAPTER FOUR

Male anti-predator services: a sexually selected form of cooperation

Filipe C.R. Cunha[1], Gretchen F. Wagner[1] and Carel P. van Schaick[1]

The evolution of acts of assistance towards unrelated individuals without evidence of reciprocation in kind ("services") has been an enduring puzzle for evolutionary biologists. Consistent sex differences in the provision of such services would suggest they arose through sexual selection. Here, we test this idea across primate species in one class of cooperative behavior: group defense against predators. We collected published data on vigilance, mobbing, and counter-attacks to assess if there is a predominant sex bias in these behaviors. We further examined whether the observed patterns could be explained by the species' mating system, while controlling for sexual dimorphism, predator type, and travel substrate. Our results demonstrate a highly prevalent male bias in anti-predatory behaviors, indicating that such services are not reciprocated in kind but should bestow other benefits to males. We suggest that this class of cooperative behaviors evolved through sexual selection.

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Introduction

The evolution of cooperation between unrelated individuals in many animal species has been a long-standing puzzle for evolutionary biologists. The evolutionary stability of non-kin cooperative behavior was traditionally thought to arise through contingent reciprocity, which involves the alternation over time of providing and receiving benefits (Trivers 1971). Yet, empirical evidence of reciprocal cooperation is rare among non-human animals, and largely restricted to reciprocation on short timescales (Hammerstein 2003, Krams et al. 2008). Acts of assistance without evidence of reciprocation in kind (henceforth: services) remain unexplained.

If services are systematically provided by one sex only, they likely arose through sexual selection (Darwin 1871). Services directed at one or many others can be designed to convey honest information about the signaler's quality (Zahavi 1995; Gintis et al. 2001). Moreover, the more costly a signal is, the more reliable it is likely to be (Zahavi 1975). When speaking of costly signals we usually think of ornaments, but they can equally be services provided specifically by males. Services directed at one or many others can be designed to convey honest information about the signaler's quality, either its physical features (Zahavi 1995) and/or its value as a cooperative partner or mate (Gintis et al. 2001). Indeed, any persistent sex bias in the provision of services would be likely to involve benefits in the form of mating access (Zahavi 1995; Taborsky et al. 2008). The provision of services to a female audience as a signal of male quality is receiving increased attention in humans (Iredale et al. 2008, Raihani and Smith 2015), but these services have only rarely been considered as explanations of male-biased cooperative acts in non-human animal behavior (Regelmann and Curio 1986, Dugatkin and Godin 1992, Cunha et al. 2017).

One common context of cooperation in primates is group defense against predators, which is predicted to have important ecological and evolutionary effects (Isbell 2005). Anti-predatory behaviors such as vigilance, mobbing and counter-attacking are adaptations aimed at reducing the risk of predation (van Schaik and Dunbar 1990, Goodman et al. 1993, Treves 1999, Zuberbühler and Jenny 2002). Given that these

behaviors are costly and can be risky, resulting in decreased foraging time, injury, or even death (Caro 2005), they represent a good opportunity for males to provide services.

All individuals should have a vested interest in staying alive. Yet, there is some empirical evidence of males performing anti-predatory behaviors at a greater rate than females in birds (Regelmann and Curio 1986, Cunha et al. 2017). Likewise, although females generally outnumber males in primate groups (Mitani et al. 2012), reports of female-biased anti-predatory behavior are rare, except in the context of direct self- or infant-defense (Corrêa and Coutinho 1997, Perry et al. 2003, Quintino and Bicca-Marques 2013). Moreover, in some primate species, males have been shown to be more vigilant, more likely to detect hidden predators (van Schaik and van Noordwijk 1989, Koenig 1998), and more likely to mob predators than females (Gursky 2005). In baboons (Cowlishaw 1995) and chimpanzees (Boesch 1991), male-led coalitions can drive off, and even kill leopards, even though single males can be predated by leopards. Accordingly, high predation risk may lead to more males in mixed-sex groups, independent of group size (van Schaik and Hörstermann 1994).

The aim of this paper is to determine whether males provide anti-predatory services in primates and, if they do, how the strength of this bias relates to mating systems. For that, we collected published observational and experimental studies on vigilance, mobbing, and counter-attacking in primate species. A systematic sex bias in these behaviors would indicate that these services are sexually selected. Within this framework, we predict that a male bias in the provision of these services should be less pronounced where opportunities for female choice of mates are restricted, e.g., in monogamous systems.

When testing these predictions, we control for sexual dimorphism, travel substrate, and predator type, as these factors may influence the risk of engaging in vigilance, mobbing, and counter-attacking. Sexual size dimorphism may play a role in male participation in anti-predatory behaviors, since the larger males are relative to females, the more likely they are to be able to protect smaller group members without incurring greater

risk. Furthermore, arboreal species have greater access to refuges than terrestrial species and therefore may be able to afford different risk levels. Similarly, the risk posed by distinct predator types can differ among group members. Therefore, these factors may also affect sex-specific engagement in anti-predatory behaviors.

Methods

Data collection

We conducted a thorough search for publications on anti-predator behavior in primates, in which we could quantify the relative participation of each sex. Studies included in the data set met the following criteria: i) describe vigilance behavior, mobbing, or a counter-attack, ii) mention the predator type (in the case of mobbing and counter-attacking), and iii) the sex of the participants. For each species included in the study, we also collected the following life-history variables: average adult male body mass, average adult female body mass, average group size, average group composition, mating system, and travel substrate (arboreal or terrestrial) (Gautier-Hion and Gautier 1976, Braza et al. 1983, Hernandez-Camacho and Defler 1985, Garber and Teaford 1986, Haltenorth and Diller 1988, Rodríguez and Boher 1988, Sussman 1991, Buchanansmith 1991, Niemitz et al. 1991, Gevaerts 1992, Ford and Davis 1992, Ford 1994, Rowe 1996, Smith and Jungers 1997, Delson et al. 2000, Wich and Nunn 2002, Mittermeier et al. 2013, Myers et al. 2008). Studies on captive animals were excluded.

We limited our search to material published before 2015. We used the following scientific citation indexing services: Google Scholar, Web of Science, Scielo and PubMed. We also consulted libraries for volumes of Folia Primatologica and the Journal of Anthropology not available online and the Primate volume of the Handbook of Mammals (Mittermeier et al. 2013). We further searched the reference list of each paper included to identify studies that were missed in the initial search. The final list of studies and of the species present in the data set is given in Appendix 4.1.

For anti-predator behaviors we used the following definitions. Vigilance was defined as an individual visually scanning its surroundings. Reports of vigilance following a predator encounter were excluded, as it is fundamentally different from vigilance in the absence of a predator and is likely to involve different mechanisms and consequences (Caro 2005). We considered mobbing to be deliberate actions directed toward potential predators (Hartley 1950, Shields 1984). We considered a counter-attack to be any active defensive behavior exhibited in direct response to a predator attack (i.e., attacking, capturing and/or killing an individual). Usually in these cases a member of the group was in direct interaction with the predator.

Statistical Analyses

We built an index based on the relative participation of individuals of each sex in each anti-predator event (Sex Bias Index, hereafter SBI). For vigilance, the data presented in the original papers were the percentage of time or samples that individuals spent vigilant, and we used the average values for each sex to calculate the SBI. To create a single value per species that represents the difference between the sexes in vigilance, we first subtracted the female values from the male values ($V_m - V_f$). We then divided this by the total mean vigilance ($SBI_{vigilance} = \frac{(V_m - V_f)}{[(V_m + V_f)/2]}$).

For mobbing and counter-attacks we estimated the expected participation of each sex according to the proportion of adult males and adult females in the group composition reported in the study; where this information was not available we used the average group composition for the population or species concerned. We then assessed the observed proportion of participation by each sex during the anti-predator event. The observed values were divided by the expected values (O/E) for each sex ("m": males; "f": females: $X_m = \frac{m_o}{m_e}$, and $X_f = \frac{f_o}{f_e}$). Finally, we subtracted the female O/E value from the male O/E value ($SBI_{mobbing/counter-attack} = X_m - X_f$). Therefore, for each behavior, an SBI value of 0 indicates no difference between the sexes (no bias). Negative numbers indicate a female

bias and positive numbers indicate a male bias, with the strength of the bias increasing as the values deviate from zero.

To test the patterns of SBIs across primates, we used the software R 3.3.0 (R Core Team 2016). We first tested whether the SBIs of vigilance, mobbing and counter-attacks were significantly different from zero (no bias), or had an overall positive (male bias) or negative (female bias) trend. For that we carried out Wilcoxon signed rank tests with continuity correction for each behavior. Then, we assessed how life-history and ecological factors influence the sex bias in anti-predator behaviors (vigilance, mobbing, and counter-attack) using phylogenetically controlled (Arnold et al. 2010) Linear Mixed Models with the Monte Carlo Markov Chain (MCMC) technique in the package MCMCglmm (Hadfield 2012). We ran separate models for each type of behavior (vigilance, mobbing, and counter-attack) using the SBI as the response variable. We included the following species-specific explanatory variables in each model: mating system (monogamous, polyandrous, polygynandrous, polygynous), travel substrate (arboreal or terrestrial) and sexual dimorphism (average adult male body mass divided by average adult female body mass). Models investigating mobbing and counter-attack behavior additionally included the predator type (snake, mammal, bird). To control for possible phylogenetic non-independence, we included a consensus tree (Arnold et al. 2010) of phylogeny as a random effect in all mixed models. The SBIs of mobbing and counter-attacking were transformed by taking the cube root, which resulted in reasonably normally-distributed residuals and does not change the interpretation of the SBI values.

We carried out the MCMC linear mixed models with a burn-in period of 100,000 iterations, a total of 1,000,000 iterations, and a thinning interval of 900 iterations. Our models resulted in acceptable effective sample sizes for all factors (~1000), indicating proper mixing of the model, which was confirmed through inspection of trace plots. Autocorrelations between iterations were acceptably low. We tested specific *a priori* predictions and thus retained non-significant terms in the models.

Results

Overall we identified 54 studies that reported 65 quantitative estimates of anti-predator behavior (vigilance, n=19; mobbing n=23, and counter-attack, n=23, Appendix 4.1). Our sample contained anti-predator behavior in 39 primate species distributed over 12 families. All of the anti-predator behaviors examined here showed a strong male bias. The SBIs of vigilance (V=176, p-value= <0.001), mobbing (V=217, p-value= <0.001), and counter-attacks (V=199, p-value= 0.003) were all significantly greater than zero, demonstrating that these behaviors are male biased in the sample as a whole (Figure 1.4a-c).

M ating system did not explain the strength of the male bias. None of the covariates included significantly influenced interspecific differences in SBI for vigilance (Table 4.1) or mobbing (Table 4.2). Regarding counter-attacks, we found a significant relationship between SBI and sexual dimorphism, such that greater dimorphism indicated a larger male bias in predator defense (Table 4.3, Figure 4.2a). Counter-attacks against a bird or a mammal were more male-biased than counter-attacks against snakes (Table 4.3, Figure 4.2b).

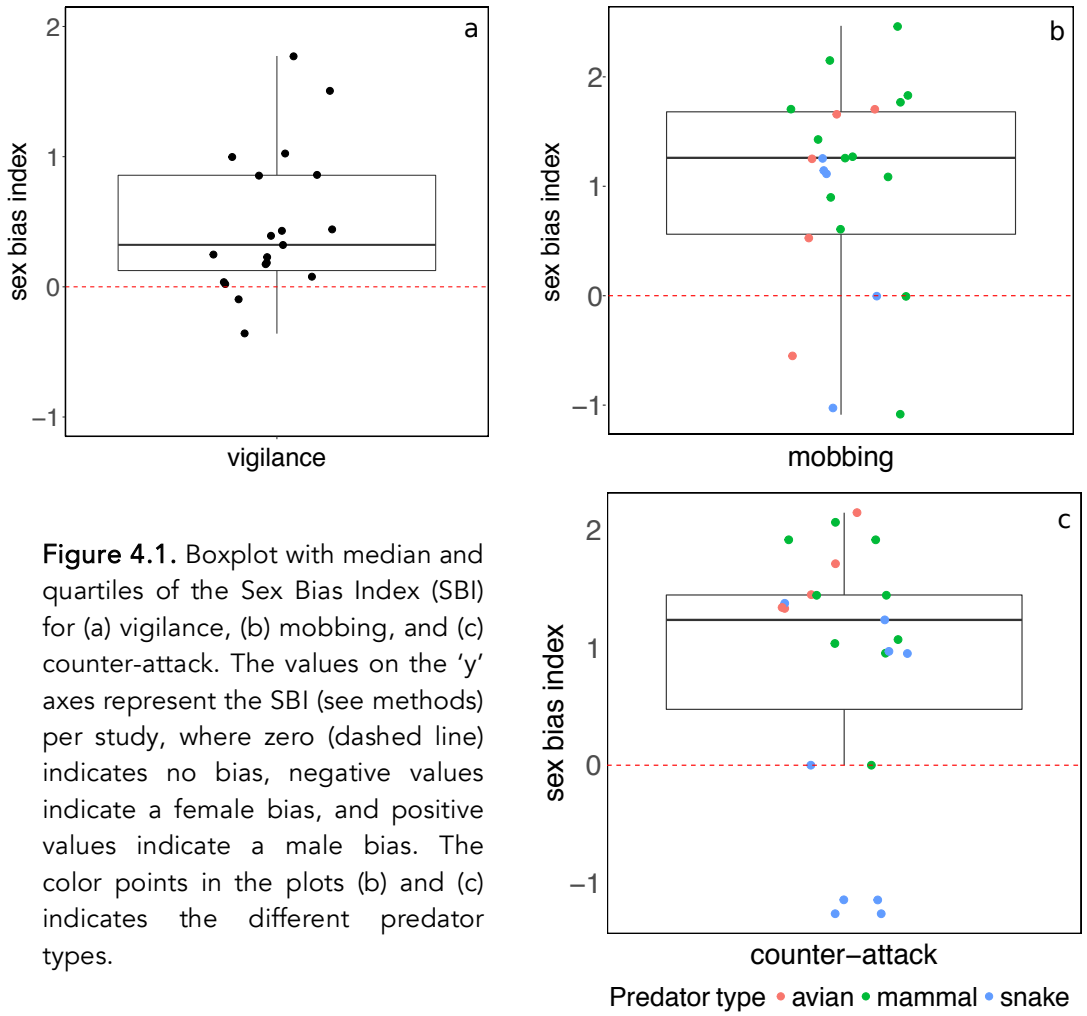

Figure 4.1. Boxplot with median and quartiles of the Sex Bias Index (SBI) for (a) vigilance, (b) mobbing, and (c) counter-attack. The values on the 'y' axes represent the SBI (see methods) per study, where zero (dashed line) indicates no bias, negative values indicate a female bias, and positive values indicate a male bias. The color points in the plots (b) and (c) indicates the different predator types.

Table 4.1. Results of phylogenetically-controlled linear mixed model comparing the effect of mating system, habitat substrate, and sexual dimorphism on the sex bias (SBI) in vigilance behavior.

factor	post mean	lower 95% CI	upper 95% CI	p- MCMC
fixed effects				
intercept	-0.319	-2.337	1.558	0.720
mating system (monogamous vs. polyandrous) †	-0.215	-1.935	1.331	0.790
mating system (monogamous vs. polygynandrous) †	0.384	-0.845	1.417	0.464
mating system (monogamous vs. polygynous) †	0.480	-0.591	1.632	0.378
substrate (arboreal vs. terrestrial) †	-0.216	-1.215	0.837	0.666
sexual dimorphism	0.361	-1.301	1.918	0.642
random effects				
phylogeny	0.230	0.000	1.084	

† Reference level is the first category in these lists.

Table 4.2. Phylogenetically controlled generalized linear mixed models comparing the effect of mating system, habitat substrate, sexual dimorphism and predator type on the sex bias (SBI) in mobbing behavior.

factor	post mean	lower 95% CI	upper 95%CI	p-MCMC
fixed effects				
intercept	1.739	-1.541	5.464	0.346
mating system (monogamous vs. polyandrous) †	-0.098	-3.279	2.641	0.958
mating system (monogamous vs. polygynandrous) †	-0.952	-2.875	1.344	0.364
mating system (monogamous vs. polygynous) †	-0.538	-2.633	1.478	0.624
predator type (bird vs. mammal) †	0.043	-1.242	1.494	0.954
predator type (bird vs. snake) †	-1.289	-3.405	0.555	0.230
substrate (arboreal vs. terrestrial) †	0.549	-1.080	2.210	0.496
sexual dimorphism	0.146	-2.636	2.639	0.918
random effects				
phylogeny	0.998	0.915	1.092	

† Reference level is the first category in these lists.

Table 4.3. Results of linear mixed model comparing the effect of mating system, habitat substrate, sexual dimorphism and predator type on the sex bias (SBI) in counter-attack behavior.

factor	post mean	lower 95% CI	upper 95%CI	p-MCMC
fixed effects				
intercept	-0.439	-3.322	2.114	0.740
mating system (monogamous vs. polyandrous) †	-0.670	-3.125	2.147	0.580
mating system (monogamous vs. polygynandrous) †	1.096	-0.388	2.377	0.114
mating system (monogamous vs. polygynous) †	0.149	-1.483	1.938	0.848
predator type (bird vs. mammal) †	-0.004	-1.181	1.165	0.970
predator type (bird vs. snake) †	**-2.235**	**-3.116**	**-1.122**	**0.002**
substrate (arboreal vs. terrestrial) †	-0.227	-1.522	0.984	0.748
sexual dimorphism	**1.837**	**0.218**	**3.735**	**0.044**
random effects				
phylogeny	2.249	0.063	4.816	

† Reference level is the first category in these lists.

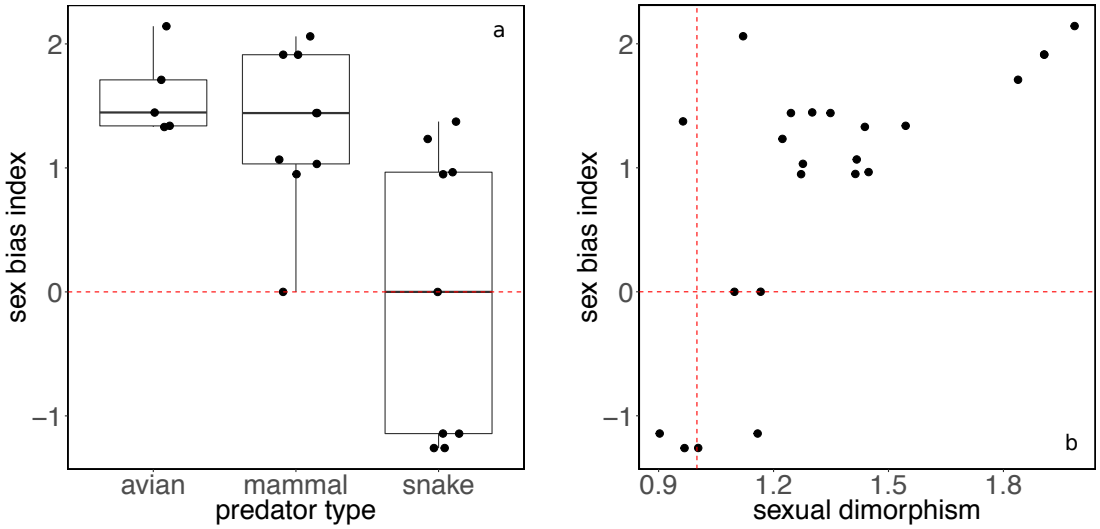

Figure 4.2. Males and females present different counter-attack patterns according to (b) the predator type and (c) sexual-dimorphism. The values on the 'x' axes represent the SBI (see methods) per study, where zero (dashed line) indicates no bias, negative values indicate a female bias, and positive values indicate a male bias.

Discussion

This broad interspecific comparison empirically demonstrated the pervasiveness of male-biased participation in anti-predatory behavior among primates. We found that males generally assume the main roles in vigilance, mobbing, and counter-attacking, supporting our prediction that these are sexually selected services. There is no evidence of reciprocation in kind by either receivers or observers of such services. Therefore, this prevalent male bias indicates that such services would not be predicted by direct or indirect reciprocity, as they are provided indiscriminately to all members of the group rather than conditionally targeted at cooperative individuals. Instead, it suggests that providing group-beneficial services imparts benefits to males beyond reciprocation in kind, probably in the form of mating access. Similar unreciprocated risk-taking behavior of males has been observed in other vertebrates, such as fishes or birds (Regelmann and Curio 1986, Giles and Huntingford 1984, Piper 1990, Cunha et al. 2017).

Surprisingly, the mating system did not influence the strength of male bias for any behavior tested. If male provision of anti-predatory services results in greater mating opportunities, we expected that the male bias would be stronger among species with

greater immediate female choice (e.g., multi-male groups). However, if females value cooperative behavior *per se*, services may have intrinsic value that surpasses their role as indicators of male vigor (Smith and Bird 2005), such as a male's potential for commitment to a partnership or parental care. Thus, females of all species may favor costly signals that specifically indicate cooperative tendencies (Gintis et al. 2005) (and predict an individual's ability to produce similar behaviors in the future), regardless of the mating system. If so, the selection pressure promoting male services would be substantial, potentially causing these behaviors to be highly prevalent, as observed in this study.

Detection of a predator is a prey's first step to avoid predation. Vigilance represents an important and persistent cost, as the time spent vigilant cannot be dedicated to searching for food, socializing, or other important activities (Caro 2005). However, when an individual is vigilant the likelihood of being surprised by predators is reduced, so although costly, vigilance is not necessarily inherently risky. We found a male bias in vigilance behavior across primate species and none of the factors tested were related to this bias. Instead, it is rather ubiquitous. An alternative explanation for a male bias in vigilance is that this behavior can be used for social monitoring of competitors or potential mates (Hirsch 2002, Favreau et al. 2010). However, social monitoring cannot explain the sex bias in mobbing and counter-attacking. Moreover, social monitoring is not mutually exclusive of anti-predatory behavior.

Anti-predatory behaviors promote the survival of the individual and/or all group members, but can also put the actors at risk (Boinski et al. 2000). Once a predator is detected, a potential prey can attempt to move the predator away by deliberately approaching and harassing it (i.e., mobbing) (Curio et al. 1978a). Mobbing occurs less frequently than vigilance, but is riskier, as it requires a prey to approach a predator, potentially resulting in injury or death (Tórrez et al. 2012). Moreover, despite the prey's best attempts to avoid predator attacks, predators can overcome these defenses. Counter-attacks are immediate, defensive reactions to a predator's strike and are frequently a response to an unanticipated attack. Counter-attacking a predator can be even riskier than

mobbing one, as the predator is highly motivated to secure its prey and may take additional victims. We found a prevalent male bias for both mobbing and counter-attacks, although the relative influence of the covariates tested on the strength of the male bias differed.

Primates can recognize their predators (Zuberbühler 2000, Fichtel and Kappeler 2002), and we found that the predator type partially influenced the male bias in counter-attack behavior: the male bias was stronger against birds and mammals, and weaker against snakes. Snakes are more likely to attack infants and juveniles (Ferrari and Ferrari 1990; Corrêa and Coutinho 1997; Ferrari and Beltrão-Mendes 2011), do not actively chase their prey over long distances, and above all are less dangerous when they are already preoccupied with a prey (i.e., less likely to attack additional individuals). Thus, it is not surprising that females – presumably mothers (Corrêa and Coutinho 1997, Perry et al. 2003, Quintino and Bicca-Marques 2013) – engage in defensive behavior against snake attacks. In contrast, avian and mammalian predators can present a constant danger to all members of the group, as they actively move through the environment, can take large prey, and can take additional prey after having struck one.

Sexual size dimorphism did not influence the strength of the male bias in vigilance or mobbing. However, our results suggest that species with greater sexual size dimorphism have a stronger male bias in counter-attacks. Given that counter-attacking is the most risky of the behaviors we examined, a strong male bias in this behavior may have particularly evolved in those species where males are best equipped to defend against threats.

Additionally, our results indicated that travel substrate did not influence the strength of male bias for any of the behaviors we examined. Arboreal and terrestrial species are likely to be subjected to different predation risks, but evidence of different predation rates has not been convincing (Isbell 2005). Therefore, the evolutionary pressure on providing anti-predatory male services may not differ greatly between terrestrial and arboreal species.

Our study indicates that males provide an important service in primate groups, as they are more actively engaged in costly behaviors and therefore more frequently exposed to high-risk situations. Honest signaling through anti-predatory behavior may offer the best explanation for the evident male bias in those behaviors and for the evolution of male services in cooperative societies. This signaling may convey information regarding male vigor (i.e., handicap principle (Zahavi 1975)), and/or express the male quality as a cooperative partner (Gintis et al. 2001). It may even represent an alternative reproductive tactic (Taborsky et al. 2008), whereby males compensate for undesirable phenotypic traits by providing anti-predatory services. Intraspecific experiments that explore individual variation in the provision of anti-predatory services and their fitness consequences would help to understand how this consistent male bias arose.

A plausible alternative explanation is that anti-predatory behaviors by males reflect paternal care. However, although male parental care may be involved in the expression of these behaviors, it is unlikely to be a general explanation, given that females have more certain parenthood, and should therefore be expected to be more active in offspring defense. Moreover, male parental care does not explain the riskiest form of anti-predatory behavior, multi-male counter-attacks in various species in which many males participate with similar contributions (e.g., Boesch 1991, Cowlishaw 1995). Finally, we noted that in at least one case (Baldellou and Peter Henzi 1992) a male that recently joined a group (and thus unlikely to have sired any offspring yet) behaved similarly to males with long group membership.

In sum, these findings provide novel evidence for the evolution of a form of sexually selected cooperation. However, the pathway through which sexual selection is acting remains unclear. Males providing services may be advertising their phenotypic quality (honest signaling) or compensate for undesirable phenotypic traits (alternative mating tactic) (or may even do both). Empirical validation of the hypothesized link between male services and fitness as well as experimental demonstration that female preferences for

males providing such services would allow us to draw stronger conclusions regarding the evolutionary mechanisms for this pattern.

APPENDIX CHAPTER FOUR

Appendix 4.1

List of studies used on the dataset of chapter four- Male anti-predator services: a sexually selected form of cooperation (Table A4.1).

Table A4.1. References from which the data for this study was extracted.

Ref.	English Name	Behavior	Predator-type	Species
1	wedge-capped capuchin	vigilance	NA	Cebus olivaceus
2	white-faced capuchin	vigilance	NA	Cebus capucinus
3	wedge-capped capuchin	vigilance	NA	Cebus olivaceus
3	wedge-capped capuchin	vigilance	NA	Cebus olivaceus
4	Thomas's langur	vigilance	NA	Presbytis comata
5	Saddleback Tamarin	vigilance	NA	Saguinus fuscicollis
5	Moustached tamarin	vigilance	NA	Saguinus mystax
6	white-faced capuchin	vigilance	NA	Cebus capucinus
7	vervet monkey	vigilance	NA	Chlorocebus aethiops
8	white-faced capuchin	vigilance	NA	Cebus capucinus
8	ring-tailed lemur	vigilance	NA	Lemur catta
9	Yellow Baboon	vigilance	NA	Papio cynocephalus
10	Ursine Colobus	vigilance	NA	Colobus vellerosus
11	Mitred Leaf Monkey	vigilance	NA	Presbytis melalophos
12	Spider Monkeys	vigilance	NA	Ateles geoffroyi
13	Red Colobus	vigilance	NA	Piliocolobus badius
13	Redtails	vigilance	NA	Cercopithecus ascanius
14	white-handed gibbon	vigilance	NA	Hylobates lar
15	vervet monkey	vigilance	NA	Chlorocebus aethiops
16	Campbell's monkey	mobbing	avian	Cercopithecus campbelli
16	Campbell's monkey	mobbing	mammal	Cercopithecus campbelli
17	Spectral tarsier	mobbing	snake	Tarsius dentatus*
18	Mantled howler monkey	mobbing	mammal	Alouatta palliata
19	Putty-nosed monkey	mobbing	avian	Cercopithecus nictitans
20	Kloss gibbon	mobbing	mammal	Hylobates klossii
21	Mountain gorilla	mobbing	mammal	Gorilla beringei
22	Japanese macaque	mobbing	mammal	Macaca fuscata
23	Equatorial saki	mobbing	avian	Pithecia pithecia
24	Mountain gorilla	mobbing	mammal	Gorilla beringei
25	Chimpanzee	mobbing	mammal	Pan troglodytes troglodytes
25	Western lowland gorilla	mobbing	mammal	Gorilla gorilla gorilla
26	Mantled howler monkey	mobbing	avian	Alouatta palliata
27	Chacma baboons	mobbing	mammal	Papio ursinus
28	Chimpanzee	mobbing	mammal	Pan troglodytes troglodytes

Ref.	English Name	Behavior	Predator-type	Species
29	Hanuman langurs	mobbing	snake	Semnopithecus entellus
30	Fork_marked Lemur	mobbing	snake	Phaner furcifer
30	Coquerel`s Giant Mouse Lemur	mobbing	snake	Mirza coquereli
31	Hanuman langurs	mobbing	mammal	Semnopithecus entellus
32	white-faced capuchin	mobbing	mammal	Cebus capucinus
33	Phayre's leaf monkey	mobbing	mammal	Trachypithecus phayrei
34	Saddle-Back Tamarins	mobbing	snake	Saguinus fuscicollis
35	Costa Rican squirrel monkeys	mobbing	avian	Saimiri oerstedii
16	Campbell's monkey	counter-attack	avian	Cercopithecus campbelli
36	Red colobus	counter-attack	mammal	Piliocolobus badius
37	Red colobus	counter-attack	mammal	Piliocolobus badius
38	Baboon	counter-attack	mammal	Papio ursinus
39	Grey-cheeked mangabey	counter-attack	avian	Lophocebus albigena
39	Putty-nosed monkey	counter-attack	avian	Cercopithecus nictitans
40	Red howler monkey	counter-attack	avian	Alouatta seniculus
41	Gelada baboon	counter-attack	mammal	Theropithecus gelada
41	Gelada baboon	counter-attack	mammal	Theropithecus gelada
28	Chimpanzee	counter-attack	mammal	Pan troglodytes troglodytes
42	Proboscis monkey	counter-attack	mammal	Nasalis larvatus
42	Proboscis monkey	counter-attack	mammal	Nasalis larvatus
43	Fat-tailed dwarf lemur	counter-attack	snake	Cheirogaleus medius
44	Gray mouse lemur	counter-attack	snake	Microcebus murinus
45	Moustached tamarin	counter-attack	snake	Saguinus mystax
46	Puris red howler monkey	counter-attack	snake	Alouatta seniculus
47	Buffy-tufted ear marmoset	counter-attack	snake	Callithrix aurita
48	Coquerel's Sifaka	counter-attack	snake	Propithecus coquereli
15	Vervet monkey	counter-attack	avian	Chlorocebus aethiops
49	White-faced capuchin	counter-attack	snake	Cebus capucinus
50	Spectral tarsier	counter-attack	snake	Tarsius dentatus*
51	White-faced capuchin	counter-attack	snake	Cebus capucinus
52	Capped Langur	counter-attack	mammal	Trachypithecus pileatus

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CHAPTER FIVE

Spotting the bird that cries hawk: a simple rule to overcome deception

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In nature, most signals are honest but some are used to deceive others. Deception is only evolutionarily stable if it occurs infrequently, or if the signals are varied. Here we experimentally demonstrate that Siberian jays Perisoreus infaustus, a family-living bird species, consider signaler reliability to overcome deception. Individuals may give warning calls in the absence of predators to gain access to food on neighbor territories. Experiments showed that individuals immediately seek cover and take longer to return after playbacks of warning calls of former group members compared to calls of neighbors or unknown individuals. Thus, Siberian jays evolved a simple rule to avoid deception by ignoring signals of potentially unreliable callers. This communication arms race can contribute to the evolution of complex communication systems.

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Introduction

Deception is an intriguing feature of communication systems, where signals are used to convey false information (Cheney and Seyfarth 1991). If receivers react as if these signals are honest, they will consequently pay a cost (Moller 1988). Interestingly, warning calls are often used to deceive others (Munn 1986; Cheney and Seyfarth 1988; Wheeler 2009; Flower 2011), probably because ignoring a warning call can be deadly (Munn 1986). Deceptive signals are usually structurally identical to genuine signals (Flower 2011), and thus, differentiating them can be difficult, particularly in acoustic communication. Natural selection should favor variation in the signals used to deceive (Flower 2011), or a low frequency of false calls, given that receivers may stop responding to signals that are too often used incorrectly (Hare and Atkins 2001; Blumstein et al. 2004). However, if the costs of ignoring a certain signal are too costly (e.g., warning calls) then selection should favor the evolution of strategies on the recipient side to reduce the costs of deception. Yet, it remains unknown if receivers have evolved adaptations to overcome the deceptive use of warning calls.

Previous studies have shown that individuals may ignore warning calls from individuals that repeatedly call in the absence of predators (Hare and Atkins 2001; Blumstein et al. 2004; Wascher et al. 2015). These results suggest that individuals can track the reliability of callers, an adaptation that should particularly evolve in group-living species (Wascher et al. 2015). In non-stable groups, such as mixed species flocks, it is unlikely that individuals recognize each other, making it rather difficult to identify those that use deceptive signals. Thus, in these systems, call recipients generally respond to warning calls, even if given deceptively (e.g., Munn 1986). Yet, in group-living species where the same individuals frequently encounter each other, and potentially share stakes in safety and resource defense, deception is likely to be moderated by social agents (Cheney and Seyfarth 1991), for example reputation or punishment (Boyd and Richerson 1992; Hauser 1992).

Here we test whether Siberian jays *Perisoreus infaustus*, a family-living bird species, are sensitive to caller reliability as a mechanism to overcome deception. Jays are sedentary and defend their all-purpose territories against intruding neighboring groups (Griesser and Ekman 2004; Ekman and Griesser 2016). Siberian jay groups include a breeding pair and up to five related and unrelated non-breeders (Griesser et al. 2008). Field observations suggest that individuals from neighbor groups give warning calls typically given towards perched hawks (Griesser 2008; 2009) in the absence of predators to gain access to food (Appendix 5.1). Thus, we hypothesize that jays should not respond to warning calls of unknown individuals or neighbors. However, they should always respond to warning calls from individuals whom they know and have had shared stakes (as fellow group members) in safety and resources.

Methods

This study was carried out in an individually color-banded population of Siberian jays (Perisoreus infaustus) near Arvidsjaur, Northern Sweden (65° 40′ N, 19° 0′ E). Birds in this population have been studied since 1989. Here we use data collected in August-October 2014 and 2015 in 36 groups. During autumn, they cache food to survive the 7-month long winter, which makes food a valuable resource (Ekman and Griesser 2016). Predation is the main cause of mortality in our study population and most individuals are killed by accipiter hawks (Griesser et al. 2017). Upon encountering a hawk, Siberian jays give referential warning calls that are specific to the behavior of the hawk, allowing call recipients to respond appropriately (Griesser 2009).

Recording perched hawk calls

We exposed 20 male and 20 female breeders foraging alone on a feeder to a taxidermized sparrowhawk Accipter nisus model, to record warning calls given to perched hawks. The feeders were placed 3-4m away from the predator model, and 2m away from a tree. The model was placed on a 1.5m high pole and covered with a camouflaged cloth.

Once all other group members were out of sight, the sparrowhawk model was uncovered and we recorded the calls given by the focal individual. Individuals were exposed to the hawk model for a maximum of three minutes, or until the focal individual left the experimental area. Calls were recorded with a Sony PCM-10 recorder connected to a directional Telinga Pro microphone with a 58cm diameter parabolic dish. We created playback sequences of 90sec based on these recordings, using Adobe Audition software. The recorded calls were arranged in the same order they were recorded, organized in loops of 90sec. A four second interval was inserted between the calls.

Playback experiments

We used a similar set-up as during the call recordings to assess the influence of caller identity on the response of breeders (i.e., experienced dominant group members). We placed a wireless loudspeaker 3-4m away from the feeder on the ground, and broadcast warning calls when the focal individual was alone at the feeder. We later assessed the reaction time, i.e., the time in seconds (± 0.1s) that the focal individual took to leave the feeder after the start of the playback; and the returning time, i.e., the time in seconds (± 0.1s), that the focal individual took to return to the feeder after leaving it, based on video recordings using the software ELAN (Brugman et al. 2004). We used a cut-off of 20min for the returning time.

We carried out two experiments to assess the role of caller identity on responses. We exposed breeders to call sequences of former group members and unknown individuals (Experiment I, conducted in 2014), and neighbors and unknown individuals (Experiment II, conducted in 2015). Given that Experiment I & II were conducted in different years and involved different sets of individuals, we used the unknown treatment as a baseline of response for both experiments. The unknown individual was recorded in a territory that was at least 6km away.

In Experiment I we chose six pairs of individuals that lived in the same group 2-5 years prior to the experiment. These individuals were breeders at the time of the

experiment and lived at least two territories away. To each of the twelve individuals we presented a playback sequence from i) the former group member and ii) and unknown individual, at least two days apart. The order of the playback treatments was random.

Experiment II was conducted in 2015 using 28 pairs of breeders that have never lived in the same group, but were breeders in adjacent territories at the time of the experiment. We used the same set-up as above but exposed focal individuals to playbacks of warning calls from a neighbor and an unknown individual.

Statistical Analyses

All analyses were done in the R statistical software (R Core Team 2016). We used Generalized Mixed Models in the package "lme4" (Bates et al. 2014) to test the reaction time and the returning time in response to warning calls of a former group member, a neighbor, and an unknown individual. We used a gamma log link function which best approximated the distribution of the response variables (Baayen and Milin 2015; Steson Lo 2015). We included in all models the receiver's identity as a random factor.

In addition, we separately tested if the reaction and returning times of former group members were influenced by the time that they had lived together in the same group (in years) or by their relatedness (related vs. unrelated), with generalized linear models using the "glm" function.

Results

Breeders exposed to warning calls of former group members responded faster by leaving the feeder more quickly (mean±s.d.=0.5±0.7sec) than when exposed to calls from an unknown individual (13.1±18.1sec) (Table 1.5, Figure 1.5). Moreover, they took longer to return to the feeder after exposure to warning calls of a former group member (472.1±406.7sec) than when exposed to warning calls of an unknown individual (270.3±278.3sec) (Table 2.5; Figure 1.5). Two females and one male did not return to the

feeder within the 20min time limit when exposed to warning calls from former group members.

Breeders did not differ in their responses to warning calls of neighbors versus unknown individuals (Table 3.5-4.5, Figure 2.5). Their reaction time to warning calls from neighbors (19.4±30.8sec) was similar to their reaction to warning calls from unknown individuals (16.1±17.4sec) (Figure 2.5). The time to return to the feeder after warning calls from neighbors (186.3±217.1sec) did not significantly differ from the return time after warning calls from unknown individuals (138.3±110.7sec) (Figure 2.5). One female breeder took 19.06min to return to the feeder after being exposed to a neighbor's warning call.

Further analyses only including the responses to calls of former group members showed that neither the amount of time they lived in the same group (estimate=-0.22, std.error=0.26, t-value=-0.85, p-value=0.41) nor their relatedness (estimate=0.75, std.error=0.78, t-value=0.96, p-value=0.35) influenced reaction times. Similar results were obtained regarding latency to return, where neither the amount of time they lived in the same group (estimate=-0.08, std.error=0.18, t-value=-0.46, p-value=0.65), nor their relatedness (estimate=-0.47, std.error=0.55, t-value=-0.85, p-value=0.41), influenced the response.

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Table 1.5. Generalized linear model of the reaction time (in sec) that Siberian jay individuals took to leave the feeder after being exposed to warning calls from former group members and from unknown individuals. Receiver's identity used as random factor.

factor	estimate	std. error	t-value	p-value
intercept	**-1.13**	**0.35**	**-3.21**	**0.001**
treatment (former group member vs. unknown)	**3.35**	**0.49**	**6.72**	**<0.001**
random factor	variance	std. dev.		
receiver identity	0.00	0.00		

Table 2.5. Generalized linear model of the returning time (in sec) that Siberian jay individuals took to return the feeder after leave it when exposed to warning calls from former group members and from unknown individuals. Receiver's identity used as random factor.

factor	estimate	std. error	t-value	p-value
intercept	**5.83**	**0.30**	**19.29**	**<0.001**
treatment (former group member vs. unknown)	**-0.98**	**0.27**	**-3.53**	**<0.001**
random factor	variance	std. dev.		
receiver identity	0.42	0.64		

Table 3.5. Generalized linear model of the reaction time (in sec) that Siberian jay individuals took to leave the feeder after being exposed to warning calls from neighbors and from unknown individuals. Receiver's identity used as random factor.

factor	estimate	std. error	t-value	p-value
intercept	**2.08**	**0.32**	**6.45**	**<0.001**
treatment (neighbor vs. unknown)	0.17	0.30	0.58	0.56
random factor	variance	std. dev.		
receiver identity	1.49	1.22		

Table 4.5. Generalized linear model of the returning time (in sec) that Siberian jay individuals took to return the feeder after leave it when exposed to warning calls from neighbors and from unknown individuals. Receiver's identity used as random factor.

factor	estimate	std. error	t-value	p-value
intercept	**5.22**	**0.17**	**29.42**	**<0.001**
treatment (neighbor vs. unknown)	-0.31	0.25	-1.24	0.212
random factor	variance	std. dev.		
receiver identity	0.000	0.000		

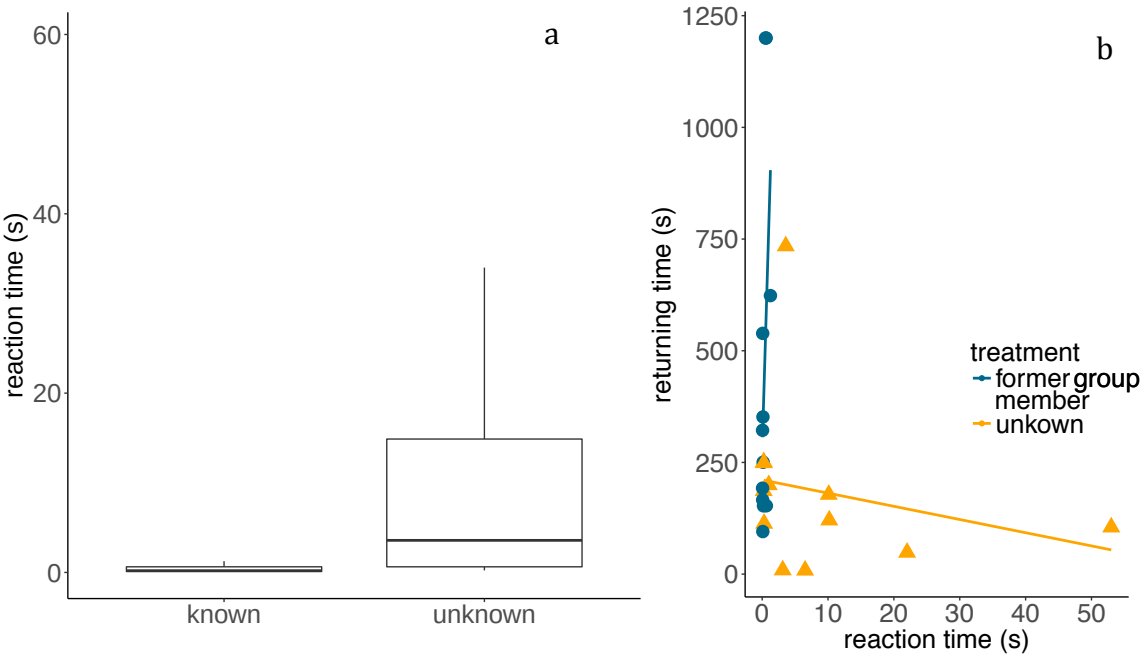

Figure 1.5. Reaction and returning time (s) of adult breeders when exposed to a broadcast of a warning call of a known and an unknown individual. (a) Boxplot reaction time after playback of a familiar individual vs. a stranger. (b) Regression lines of return latency in relation to reaction latency for warning calls of former group members (blue) and unknown individuals (orange).

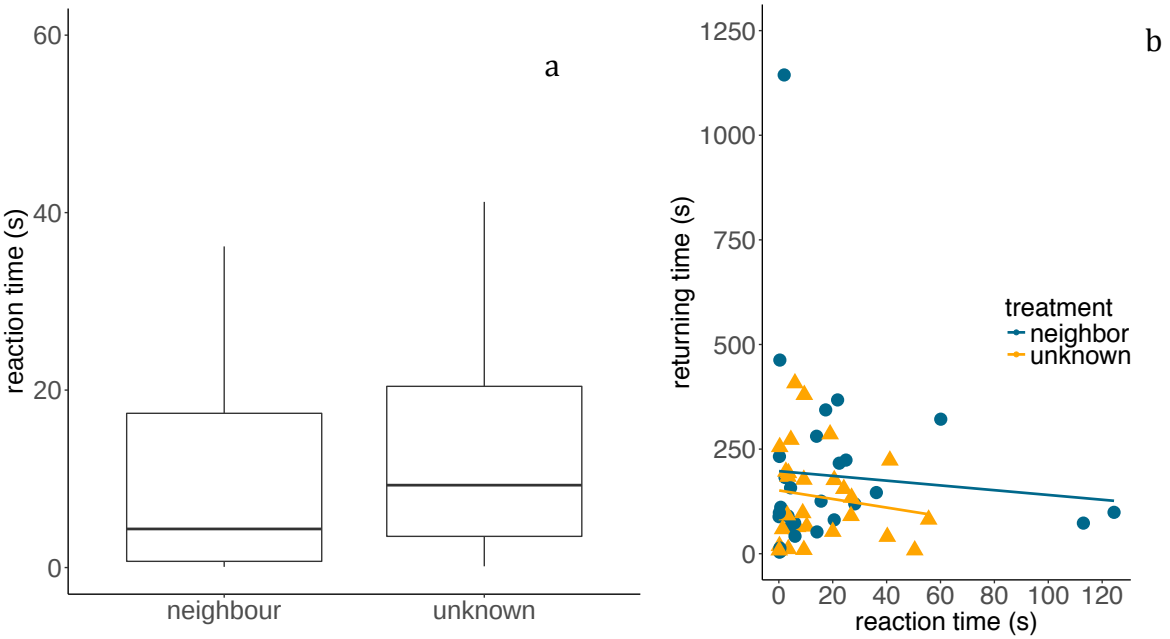

Figure 2.5. Reaction and returning time (s) of adult breeders when exposed to a broadcast of a warning call of a neighbor and an unknown individual. (a) Boxplot reaction time after playback of a familiar individual vs. a stranger. (b) Regression lines of return latency in relation to reaction latency for warning calls of neighbor (blue) and unknown individuals (orange).

Discussion

Our results demonstrate that Siberian jays show a strikingly different response when exposed to warning calls of former group members than both neighbors and unknown individuals. Jays immediately left the feeder and took longer to return when exposed to calls from former group members than when exposed to calls of neighbors or unknown individuals. These results suggest that Siberian jays trust warning calls of individuals with whom they have or had shared interests, and that familiarity alone does not influence how individuals react to a warning call. Neither unknown individuals nor neighbors share stakes in the safety of the group or in resource defense. Rather, neighbors seem to use warning calls in a deceptive manner, and thus they should not be trusted, as suggested by our results.

Siberian jays cache in late summer and autumn food in their territory for the winter to come, making their territory a valuable resource (Ekman and Griesser 2016). All group members participate in between-group encounters that can last up to 15min and escalate to vigorous chasing that is never observed within groups (Griesser et al. 2015). Thus, group members develop a shared stake by defending the territory and should have a lower interest to cheat each other than neighbors (van Rhijn and Vodegel 1980). Indeed, most observations where false warning calls were given involved individuals that intruded on a neighbor territory trying to access a feeder (Appendix 5.1). Although our results suggest that warning calls of neighbors are generally perceived as unreliable, there was a larger variance in the responses to warning calls by neighbors than by unknown individuals. This may reflect that neighbors can vary in their propensity to give false warning calls and/or to intrude on a neighboring territory. Since encounters with neighbors have been opportunistically observed, further empirical investigation to test this hypothesis are needed.

Although the use of deceptive strategies to gain benefits, at the expenses of others, is not unusual among organisms (Kiers et al. 2003; Mokkonen and Lindstedt 2016), little is known about strategies to overcome deception. In mutualistic interactions involving the

physical exchange of goods, a biological market may arise to regulate it (Kiers et al. 2003). Thus, the partner that does not receive its share of resources stops to provide its counterpart (Kiers et al. 2003). However, in situations where non-physical goods are exchanged, such as warning calls, strategies to overcome deception are unlikely to be based on biological market principles (Noë and Hammerstein 1995; Hammerstein and Noë 2016). Instead, social constraints may play a role on the evolutionary stability of deception (Cheney and Sayfarth 1991). Our findings suggest that Siberian jays use social cues to discriminate caller reliability and thus, to overcome deception.

Our results differ from a previous study (Munn 1986) that assessed vocal deception with respect to the signal that is used. While Siberian jays use a call that conveys an intermediate risk to deceive, nuclear species in mixed bird flocks use a call denoting a high-risk predator in a deceptive manner (Munn 1986). This suggests that the urgency level of the signals that are used to deceive may relate to the social constraints amongst the individuals involved (Cheney and Seyfarth 1991). In species that are unlikely to have repeated interactions with known individuals, high urgency warning calls seem to be used to deceive, given that they are too costly to ignore and unlikely to impose social repercussions. Moreover, the frequency of false warning calls seems not to play a role in these species (Munn 1986). In contrast, in interspecific interactions among known individuals, a deceiver can use signals that convey information of high-risk predators, but they need to vary the usage of these signals (Flower 2011). A persistent use of the same signal by the same individual in these interactions can elicit a receiver to be non-responsive (Flower 2011). Yet, in these cases, deception occurred between species, where shared stakes are likely to be minimal.

In species that form stable conspecific social groups, warning calls that convey information of an intermediate risk are instead used to deceive (Wheeler 2009; Wheeler and Hammerschmidt 2012, this study). In the Siberian jays, “perched hawk” calls are used in a deceptive manner, while calls that denote a higher risk, such as “prey searching hawk” or “attacking hawk” calls (Griesser 2008), have not been observed in a deceptive context.

While low-risk risk signals are unlikely to elicit a response from others. high-risk signals are too costly to be ignored, and are therefore unlikely to be used as deceptive signals in stable social systems, because persistent deception is not evolutionarily stable (Axelrod 2006; Foster and Kokko 2006). Thus, deceptive signals that convey an intermediate risk are likely to be favored by natural selection in species with stable social groups with repeated interactions between known individuals.

Acoustic warning calls are ephemeral signals, making it difficult for call recipients to assess whether a call was given in response to the associated stimuli, or is dishonest. Costly signaling theory states that the higher the costs of a signal, the higher the likelihood of it being honest (Zahavi 1975), but for ephemeral signals honesty cannot be measured by the costs of producing the signal. Thus, it can be too costly to ignore certain signals, like warning calls (e.g., Munn 1986), compelling call recipients to respond generally. Our results show that Siberian jays overcome this problem by assessing individuals' reliability based on whether they had shared interests with the caller or not. Overcoming deception by determining individual reliability may impose important selective pressure, particularly in social species that must adjust their signal, or change the conveyed information, to continue to elicit the desired response. More generally, this rule may facilitate the evolution of complex communication systems, where information is conveyed through ephemeral signals, such as language.

APPENDIX CHAPTER FIVE

Appendix 5.1

Our observations suggest that neighbors more likely to use warning calls in absence of predators than group members (chi-squared = 4.45, df = 1, p-value = 0.034) (Table A1.5).

Table A1.5. Events register of perched hawks warning calls emitted in the absence of predators during which was possible identify the deceiver, during 43 days of observation between 2015/2016.

false warning author	description
group member	adult female breeder
group member	adult related male non-breeder
neighbor	several neighbor individuals upon arrival on the neighboring territory
neighbor	several neighbor individuals upon arrival on the neighboring territory
neighbor	adult male breeder while neighbor male breeder was on the feeder
neighbor	adult male non-breeder
neighbor	adult female breeder
neighbor	adult female breeder
neighbor	unrelated adult non-breeder (unknown sex)
neighbor	adult male non-breeder (unknown relatedness)
neighbor	unrelated adult non-breeder (unknown sex)

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